Life Histories and Ecological Interactions of *Potamopyrgus antipodarum* and *Physa acuta* in Relation to Temperature

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FRONTISPIECE: PANORAMIC VIEW OF HANMER BASIN

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ABSTRACT

The New Zealand freshwater snail *Potamopyrgus antipodarum* has recently invaded freshwaters of North America and as a result its occurrence and spread have led to growing concern regarding its potentially negative impacts on members of the native fauna. These include several species of pulmonate gastropods in the family Physidae. *Physa acuta*, an endemic of Mediterranean Europe has successfully established itself in New Zealand, Australia and Africa, and occurs alongside *P. antipodarum* in a variety of Canterbury freshwaters. Its occurrence provided the opportunity to compare and examine the life histories and interactions of two highly successful invading species.

Growth, reproduction and competitive interactions between *P. antipodarum* and *P. acuta* were investigated with particular reference to water temperature at four sites (including one influenced by a geothermal source) at Hanmer Springs, North Canterbury. Field and laboratory experiments were carried out over a 12 month period from January to December 1998. Water temperature in the range 4 to 15°C had a strong effect on the growth rate of juvenile *P. antipodarum*, which grew slowly at 4°C and fastest at 15°C. In contrast, *P. acuta* was not affected by water temperature and grew at similar rates when kept at 4, 8 and 15°C. Recruitment of young occurred year round in *P. antipodarum*, whereas *P. acuta* appeared to require a higher water temperature to instigate oviposition. *P. antipodarum* from all four study sites had similar seasonal patterns in the number of embryos carried per individual female, but reproductive output differed between sites. Although large populations were sustained at the thermally influenced Site 4, reproductive output was low at all times.

Crowding by conspecifics had strong effects on growth and fecundity of both *P. antipodarum* and *P. acuta*, but similar levels of crowding by the other species stimulated growth and reproductive output of both species, most notably *P. acuta.* Furthermore, growth of juvenile *P. acuta* was stimulated in the presence of chemical substances released by adult *P. antipodarum*, indicating that it can detect a potentially competing species without physical interference. My findings indicate that *P. antipodarum* can exist at a variety of temperature regimes, but prolonged exposure to moderately high temperatures are likely to be at a cost to reproductive output and population growth. The ability of *P. acuta* (and possible other physids) to increase its growth rate and reproductive output in the presence of another snail species suggested that the presence of *P. antipodarum* in North America may not necessarily be at the expense of endemic physids at least.

CHAPTER ONE

INTRODUCTION

Two critical issues facing conservation agencies around the world are to control the spread and to deal with the effects of exotic species (Gangloff, 1998). A particular concern for endemic communities and species of conservation interest, is the introduction of species beyond their native ranges. Known variously as "exotics", "aliens", "invaders", "non-natives", or "non-indigenous species", there are many examples of disastrous invasions by such organisms that have resulted in losses of native species and changes in community structure and function (Drake et al. 1989). Examples of exotic invaders that alter aquatic ecosystems, are extensive and alarming, and include numerous species of molluscs (Richards, 1997; Nalepa & Schloesser, 1993).

Invasions of exotic molluscs around the world continue to plague native aquatic communities. In particular, many areas of North America from the Great Lakes, to coastal wetlands have become dominated by molluscan invaders (Richards, 1997). For example, introductions of the freshwater zebra mussel, *Dreissena polymorpha* and the Asiatic clam, *Corbicula flumenea*, have caused significant ecological and economic impacts in many parts of the Laurentian Great Lakes (Nalepa & Schloesser, 1993). The ability of these molluscs to exploit new habitats, together with numerous adaptations, such as planktonic larvae, high fecundities, and watertight or buoyant shells, has led to serious problems. Not only have these invaders caused economic harm such as the fouling of water treatment facilities and obstruction of irrigation canals, but ecological damage, by outcompeting native endangered molluscs (Richards, 1997).

A recent invader of freshwaters in North America, is the New Zealand snail *Potamopyrgus antipodarum* (Fig 1.1). Its occurrence and spread have led to growing concern regarding its potential negative impacts on native fauna, and the Wyoming Game and Fish Commission (1998), for example, has recently passed legislation banning the possession, importation and movement of *P. antipodarum* into or within the State of Wyoming.

The hydrobiid genus *Potamopyrgus*, is indigenous to New Zealand and is represented by three non-subterranean species. However, only the ubiquitous and morphologically highly variable *Potamopyrgus antipodarum* is found in freshwater (Winterbourn, 1970a). *P. antipodarum* is a member of the gastropod order Prosobranchia, the lungless snails, and is an unusual mollusc because it is both ovoviviparous and facultatively parthenogenetic. Sex ratios

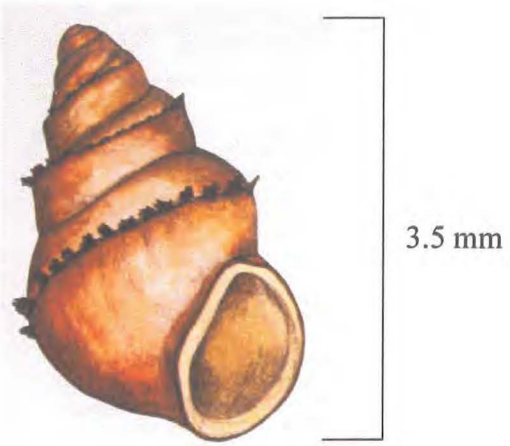


Fig 1.1 The New Zealand prosobranch gastropod *Potamopyrgus antipodarum* (from Winterbourn & Mason, 1983).

can vary from mostly females to equal proportions of males and females (Winterbourn, 1973). *P. antipodarum* is widely distributed throughout New Zealand in lakes, ponds, rivers and streams and tolerates a wide range of environmental conditions (Winterbourn, 1969, 1970b). According to Jokela & Lively (1995a), *P. antipodarum* can reproduce rapidly under favourable conditions and quickly dominate the benthic community in both lakes and rivers.

P. antipodarum has been a successful invader and is well established in Australia, the United Kingdom and much of Continental Europe (Ponder, 1988). Initially *P. antipodarum* was introduced into Europe from Australasia (Winterbourn, 1970a), and was first recorded in the River Thames, England in 1889. However, it was probably introduced as early as 1859 (Ponder, 1988) and according to Zaranko et al. (1997), within 40 years *P. antipodarum* had spread throughout England and Wales and was reported on the European mainland by 1899. By 1920 *P. antipodarum* had spread to many parts of Europe.

In 1987, *P. antipodarum* was discovered in the Middle Snake River, Idaho, and since its discovery densities have increased (Zaranko et al. 1997). Time and source of introduction are unknown, but it is speculated that the snail was inadvertently introduced from the commercial movement of aquaculture products such as trout eggs and live fish, sometime during the 1980s (Bowler & Frest, 1992). Over the past ten years the species has expanded its range from a single locality to over 640 km along the Snake River and its tributaries. *P. antipodarum* has recently crossed the North American Continental Divide, spreading into the Madison River system in the neighbouring Missouri River drainage (Bowler & Frest, 1992) and is widely distributed in Yellowstone National Park. In 1991, *P. antipodarum* were

collected from Lake Ontario, and it is thought that this invasion occurred from a source other than the Snake River population (Gangloff, 1998). Zaranko et al. (1997), speculated that they were introduced via ballast water emptied from European commercial vessels. According to Gangloff (1998) the snail has now been discovered in the Colombia River, near Astoria, Oregon (Fig 1.2). Because of the snail's ability to tolerate a wide variety of habitats and environmental conditions, and its high reproductive capacity, *P. antipodarum* will probably spread quickly throughout the Great Lakes area as it has done in Europe and Australia.

The biofouling potential of *P. antipodarum* is probably low compared with that of the zebra mussel, however, its most serious threat may be through outcompeting native molluscs for resources (Zaranko et al. 1997). Tourism and cold water trout fisheries form significant aspects of the economy of the western United States, and Montana's cold water trout fisheries have been estimated to generate over $300 million to the state's economy annually (Richards, 1997). Richards (1997) estimated that the invasion and establishment of *P. antipodarum*, in trout rivers of Montana and other parts of the United States could have severe negative effects on those areas which include significant trout fisheries. *P. antipodarum* may pass unharmed through a trout's digestive tract because of its thick shell and operculum (Gangloff, 1998), and therefore provide little nutritional value to fish that could suffer a net energy loss if they attempt to feed on it. Further, according to Allan & Flecker (1993), most of North America's freshwater mollusc populations are endangered or declining. Both competition theory and empirical data suggest that introduced exotic species are likely to cause negative impacts on native fauna and may change aspects of community structure and function. Because most snails are vegetarian grazers or omnivorous scrapers (Cummins & Klug, 1979), taxa that are most likely to be affected via competition by increasing numbers of *P. antipodarum,* are endemic snails. These include several species of pulmonate gastropods in the family Physidae.

Species of Physidae are not native to New Zealand and *Physa acuta* (Fig 1.3) has been introduced. *P. acuta* is native to Mediterranean Europe and has successfully established itself in New Zealand, Australia and Africa (Winterbourn, 1973). *P. acuta* is often found with *P. antipodarum* and may compete with it for space and food in some environments.

P. acuta is hermaphroditic and lays eggs that develop in the water. The eggs are contained in gelatinous egg masses and the juvenile snails move away from them when they reach a shell length of 0.8 to 1.0 mm (Stevenson, 1973). The occurrence of *P. antipodarum* and *P. acuta* living together in a variety of Canterbury freshwaters provides an opportunity to

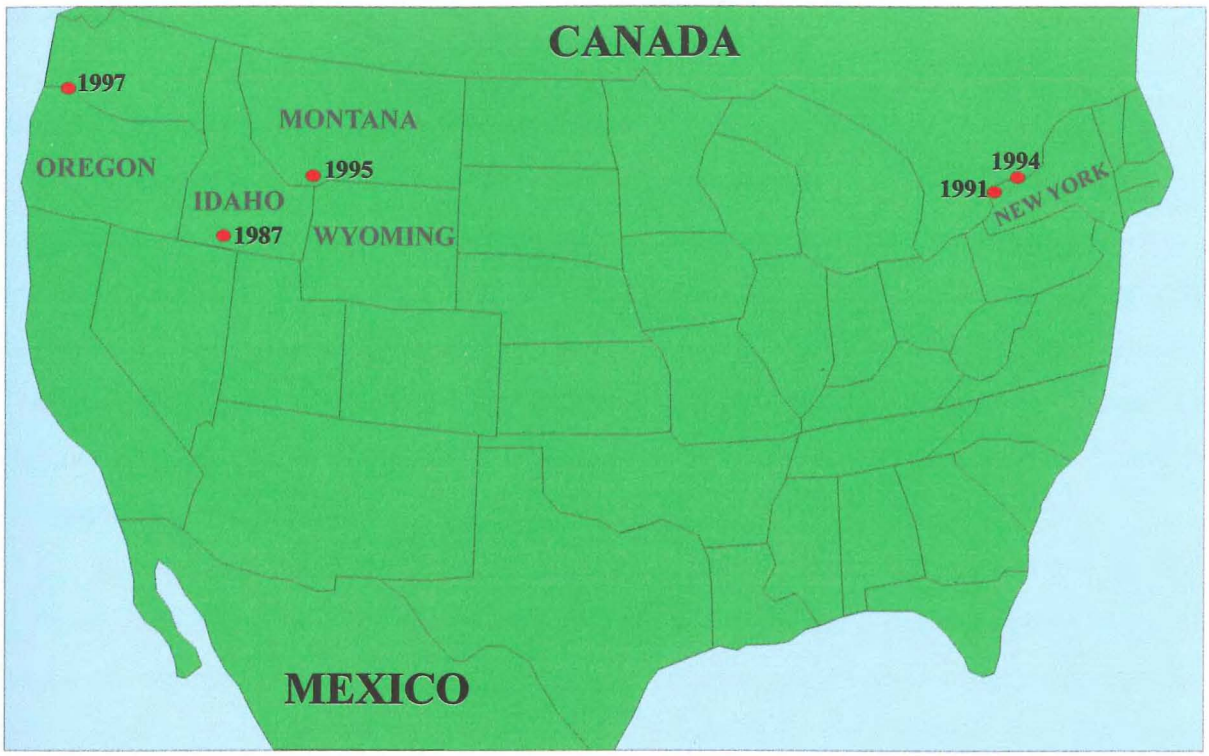


Fig 1.2 Known distribution and date of first documented occurrence of *P. antipodarum* in North America. Dates correspond to the following localities: **1987** Middle Snake River, Idaho; **1991** Lake Ontario near Wilson, New York; **1994** Lake Ontario near the St. Lawrence River origin; **1995** upper Madison River and tributaries, Montana; **1997** Columbia River at Astoria, Oregon (after Gangloff, 1998).

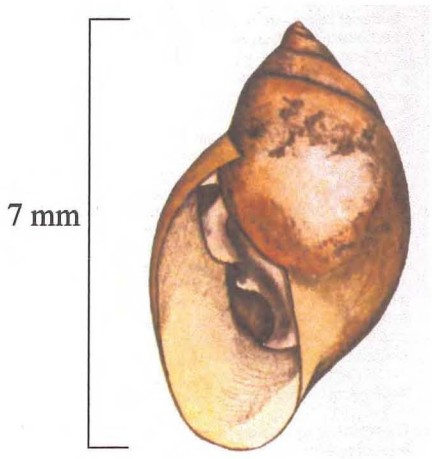


Fig 1.3 The pulmonate gastropod *Physa acuta* (from Winterbourn & Mason, 1983).

compare and examine the interactions of two highly successful invading species. Such a comparison has the potential to provide insights into the possible impacts of *P. antipodarum* on North American snail populations, where in contrast to New Zealand, *P. antipodarum* is the invader and Physidae are common endemics.

The objective of my study was to investigate aspects of growth, reproduction and competition of *P. antipodarum* and *P. acuta* with particular interest in water temperature. If reproductive activity and growth are influenced by water temperature, then it may be possible to predict the spread of these animals in North America where concern is being expressed. The study was undertaken at four sites (including one influenced by a geothermal source) in Hanmer Springs, North Canterbury, where a wide range of temperature regimes could be incorporated into the study.

In Chapter 2 the environment of the Hanmer Springs Basin is described and physico-chemical characteristics are given for the four study sites. Chapter 3 presents results of a study on the growth and reproductive biology of *P. antipodarum* and *P. acuta* under different water temperatures. This aspect of the study provided information about reproductive differences between the two snails, and possible environmental limitations on their dispersal. Competitive interactions of *P. antipodarum* and *P. acuta* are discussed in Chapter 4. According to Gangloff (1998), there has been little work on competition between *P. antipodarum* and native gastropods in North America, and although observations suggest that there may be some competition occurring, I wanted to determine at what level this was happening. Finally, in Chapter 5, my findings are considered in relation to the possible impacts *Potamopyrgus antipodarum* may have on the native *Physa* species and other freshwater fauna in North America.

CHAPTER TWO

STUDY AREA

Introduction

The study was undertaken at Hanmer Springs (42° 32'S, 172° 50'E), a small township in the Hanmer Basin, Amuri County, north-west Canterbury. Amuri County covers an area of about 500 000 hectares and Hanmer Springs is located in the centre, approximately 130 km north of Christchurch (Fig 2.1).

The township of Hanmer Springs was established in the 1860s around its geothermal springs, and in 1902, further development occurred in conjunction with the establishment of the Hanmer State Forest. Today, the Hanmer Springs Thermal Reserve is undoubtedly the flagship for Hanmer tourism, with visitor numbers pushing towards half a million people a year (Leech, 1988). Europeans first discovered the hot springs in 1859, when a Culverden farmer, William Jones, noticed a strange fog near the track along which he was walking and went to investigate.

Geology

The Hanmer Basin is formed on the Hope Fault, the southern and most active element of the 80 km wide Marlborough fault system (Wood et al. 1994). It is a spindle shaped structural depression measuring 15 km long and 7 km wide and was formed between the right step-over of two Hope fault segments, conforming closely to a traditional pull-apart basin model (Wood et al. 1994) (Fig 2.2). The basin is filled with Quaternary alluvial deposits which are surrounded by Late Jurassic to Early Cretaceous greywacke basement (Bradshaw, 1989). The greywacke forms the basis of rugged mountains that stand about 1 km above the basin.

Geothermal System

Thermal springs and streams occur most frequently in areas of volcanic activity, important ones being found in Europe, North America, (such as Yellowstone National Park) and the North Island of New Zealand (Smith, 1969). However, the Hanmer Springs geothermal system is caused by the deep circulation of meteoric (atmospheric) water through the Hanmer

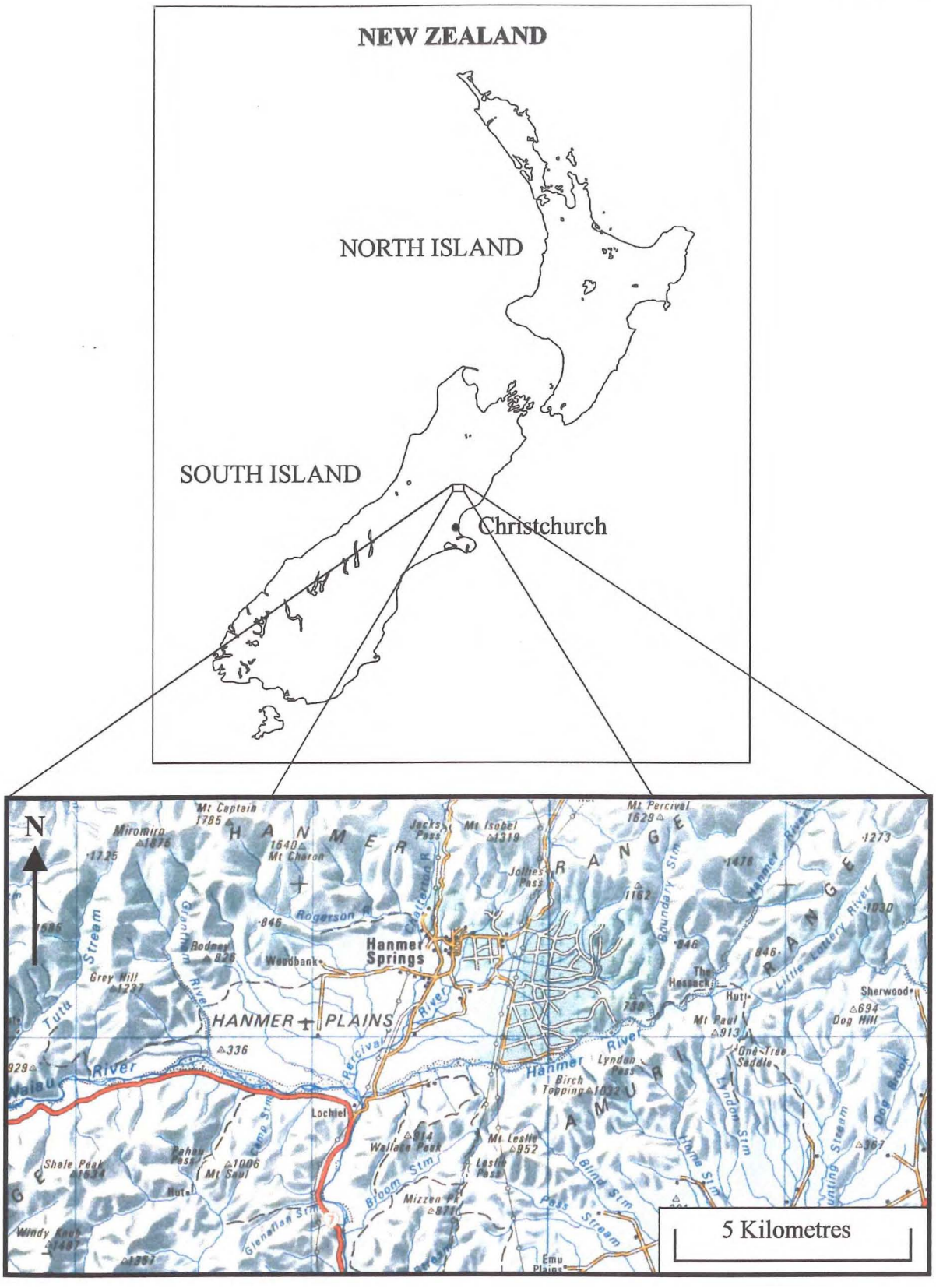


Fig 2.1 Location map of Hanmer Springs township. Topographic map taken from New Zealand Map Series 1:250,000 Sheet 11, Kaikoura.

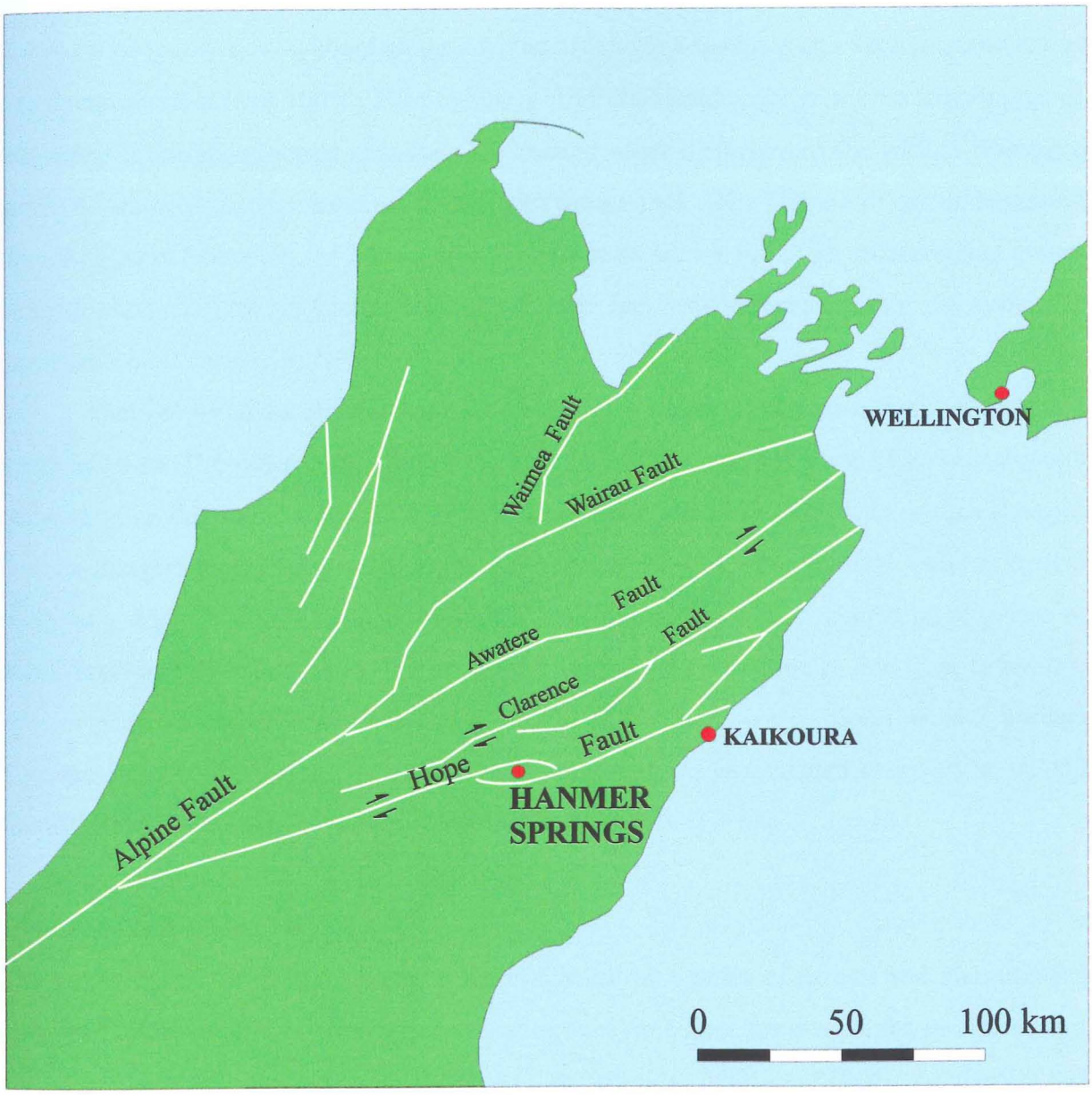


Fig 2.2 Map of the major faults in the northern part of the South Island. Hanmer Springs is situated in the Hanmer Basin, formed from two segments of the Hope Fault (after Leech, 1988).

fault zone. Leech (1988) found that precipitation falling on the Hanmer ranges immediately to the north infiltrated through fractures in the basement. The infiltrating rainwater becomes hotter the deeper it moves, circulating to depths of 2.5 km where it mixes with groundwater at a temperature of at least 100°C. Heat radiating from the earth's core raises the temperature of rainwater in the underground reservoir. The heated water then rises to the surface through a series of interconnecting fractures in the greywacke rock. The chance of an underground fracture system extending for 2 km without interruption is rare, but is the situation that occurs beneath Hanmer Springs. Circulating groundwater has resident times within the system in excess of 40-50 years (Fig 2.3).

Thermal water for the hot pools is drawn from a bore drilled into fractured rock to a depth of 18 m. The water comes out of the bore at 54°C having lost some of its heat through convection on the way to the earth's surface. Heat is extracted from the water using a series of heat exchangers to maintain water in the hot pools at 32-40°C. The thermal water is treated minimally. First it passes through a series of gauze strainers which remove large pieces of debris such as leaves and twigs. It then passes through an exceptionally fine filter to remove smaller particles and chlorine is added at a ratio of two parts per million (Hanmer Springs Thermal Reserve Pamphlet, Undated). The thermal water is recirculated every 34 hours and finally released as waste into nearby Hospital Creek (Fig 2.4) (Plate 2.1a & b).

Landscape and Vegetation

The landscape of the Hanmer Basin is the end result of a series of natural and man-induced changes (Malcolm, 1984). Geological activities over time have resulted in the upthrusting of the mountain ranges that surround the basin. According to Malcolm (1984), weathering and erosion have worn the mountain ranges down to their present form, cutting valleys and gullies, infilling basins and providing the material from which the lowlands are formed.

The geological structure together with climate also influences the vegetation cover of the land. There is a natural vertical gradient of vegetation types at Hanmer, ranging from tussock grassland on the basin floor, through beech stands and exotic forest on the hill slopes, to mountain shrub at 1500 m (Washbourn, 1984). Human influence has greatly altered the range of plant species growing in the Hanmer area. For example, Washbourn (1984) reported that many streams flowing through the area have now been lined with willows and poplars.

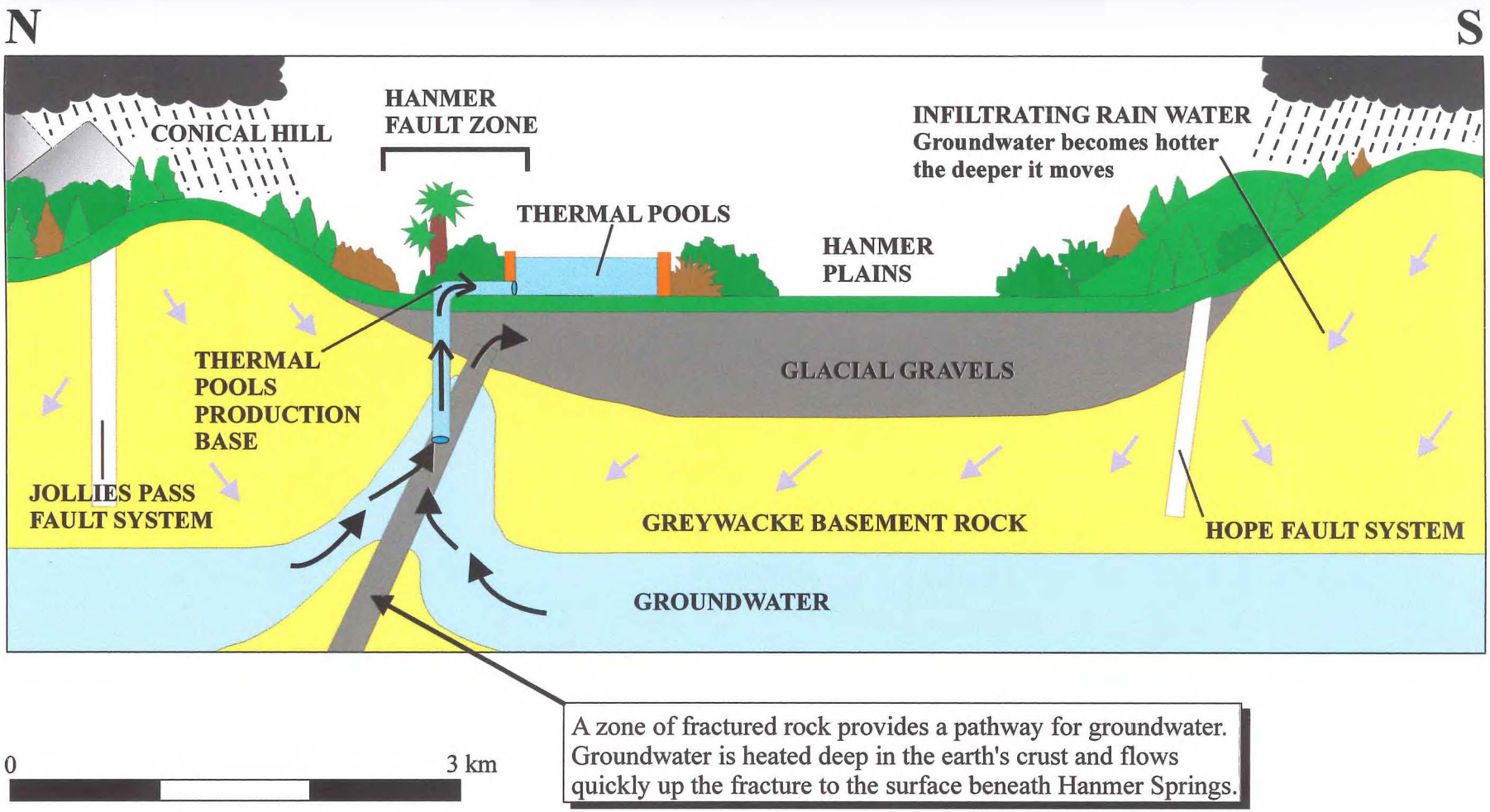


Fig 2.3 A simplified cross-section showing the geological setting of the Hanmer Springs region, and the cycle that generates the geothermal water (from Hanmer Springs Thermal Reserve pamphlet, undated).

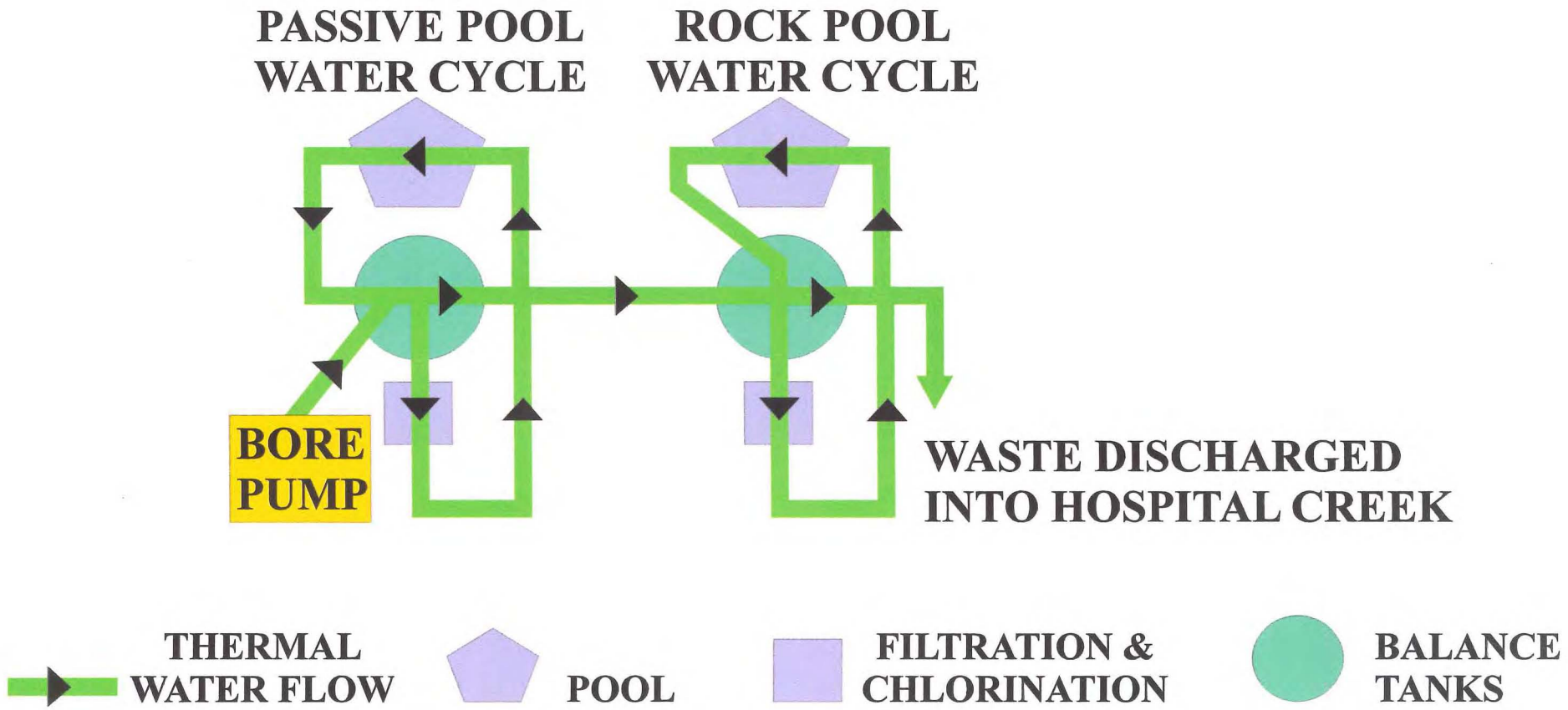
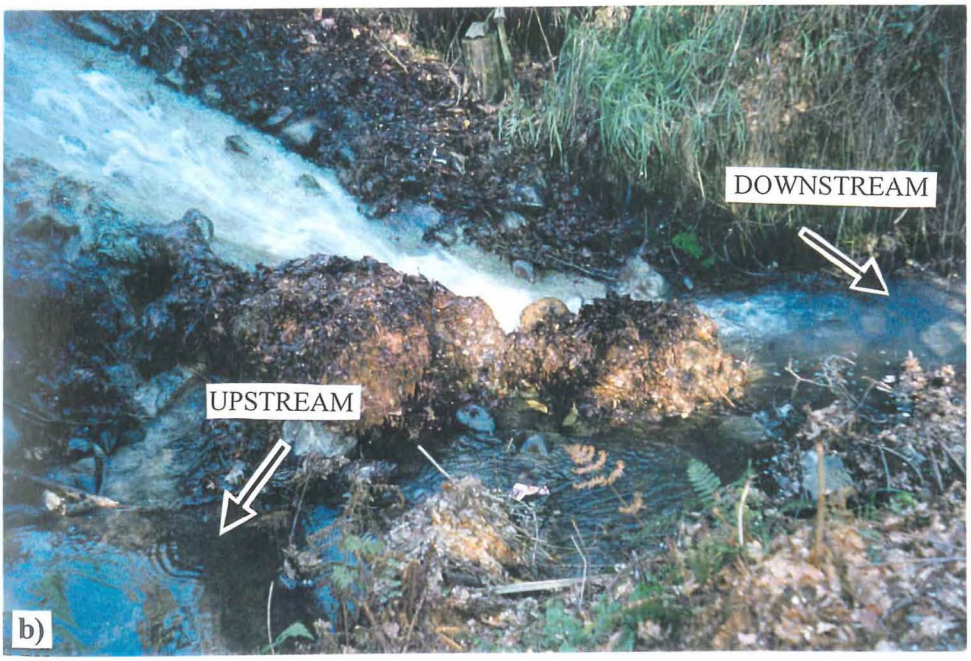


Fig 2.4 Flow diagram showing the process of water treatment within the hot pools at Hanmer Springs (from Hanmer Springs Thermal Reserve pamphlet, undated).

Plate 2.1 a) Thermal effluent pipe draining the hot pools.

b) Thermal effluent entry point into Hospital Creek.



Beech forest has also been cleared, and in many cases the cleared areas have been recolonised by native alpine shrub and exotic forest. In summary, the Hanmer Basin incorporates a mosaic of contrasting vegetation types, introduced, indigenous and man modified.

Climate

Weather patterns at Hanmer are distinctive. Southerly winds normally bring rainfall to the region and are frequently accompanied by snow at high altitudes (Malcolm, 1984). Hanmer may experience long dry periods in summer from December to March, and frosts occur frequently during the winter months of May to August. Snow usually falls on a few days each year around the Hanmer township, but rarely lies on the ground for more than a few days (Malcolm, 1984).

During the period of my study, the highest average monthly air temperature recorded at Hanmer Springs was 19.6°C in February, the lowest 4.8°C was recorded in June and August (NIWA climate records, pers. comm.). Compared with temperature data obtained from the last ten years, 1998 was a warm year, as average monthly temperatures were higher in all months except August and November (Fig 2.5a).

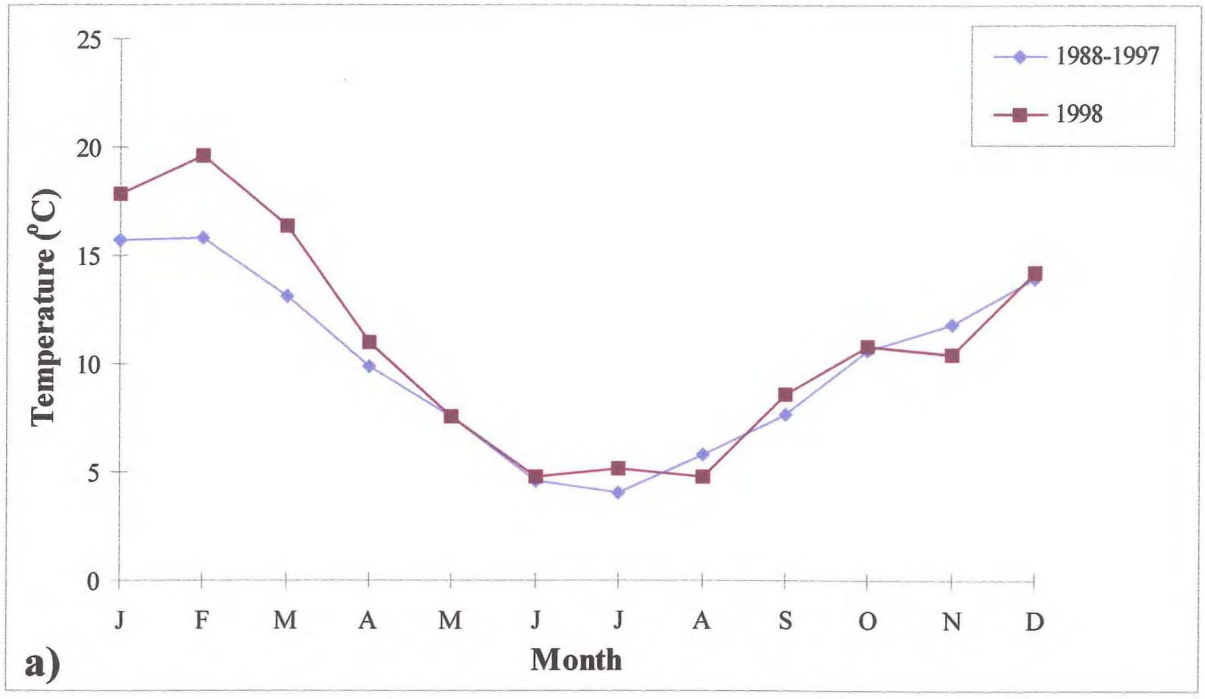
1998 was not only warmer on average, it was also very dry. During the 12 months of my study, monthly rainfall totals were considerably lower (except July and October) than the average recorded for the past ten years. Rainfall was lowest in February when only 16 mm were recorded. Rainfall increased in winter, but the highest value (140 mm) was recorded in October (NIWA climate records, pers. comm.) (Fig 2.5b).

Study Sites

The four study sites were located close to the Hanmer Springs township and were chosen in order to include a range of temperature regimes and physico-chemical factors.

Site 1 - Switchback Stream

Site 1 was on Switchback Stream, a cool, mountain fed stream that flows through the Forest Camp approximately 2.5 km from the town centre (Fig 2.6). Switchback Stream is a small first order stream whose source is a spring about 700 metres a.s.l. Situated 30 km downstream from the source, Site 1 was within a low-gradient reach bordered by mixed scrub and willow



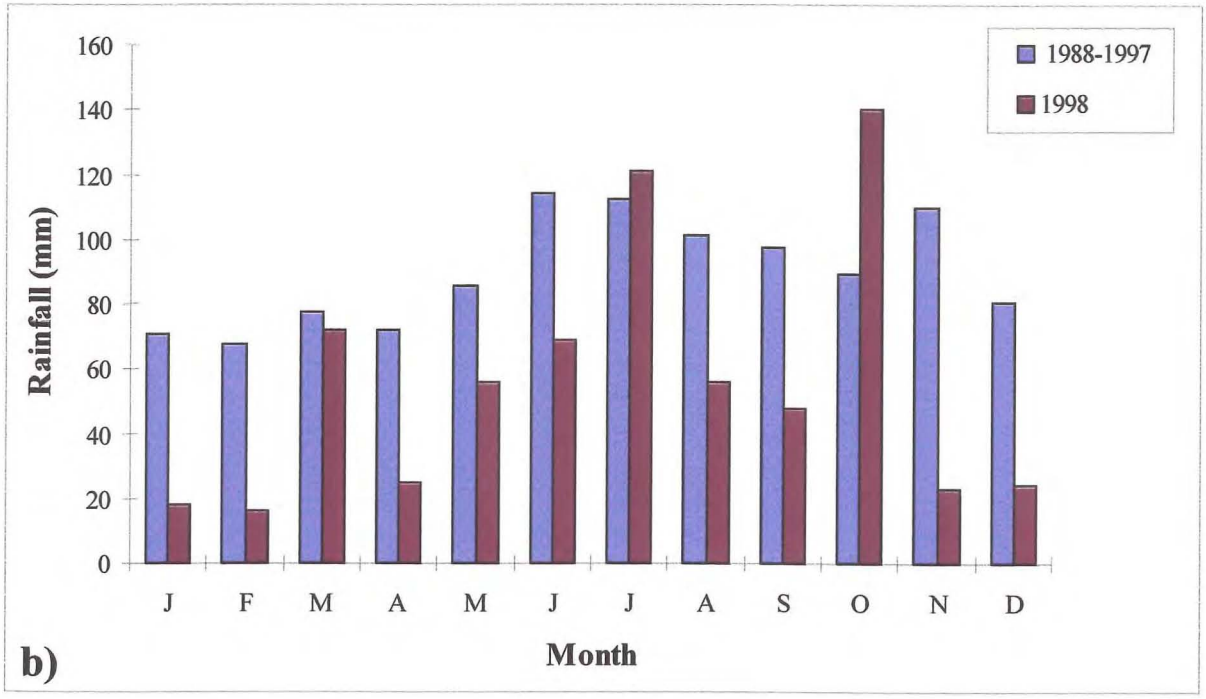


Fig 2.5 **a)** Average monthly air temperatures at Hanmer Springs for1998, compared to averages for 1988-1997.

b) Monthly rainfall totals at Hanmer Springs for 1998, compared to averages for 1988-1997.

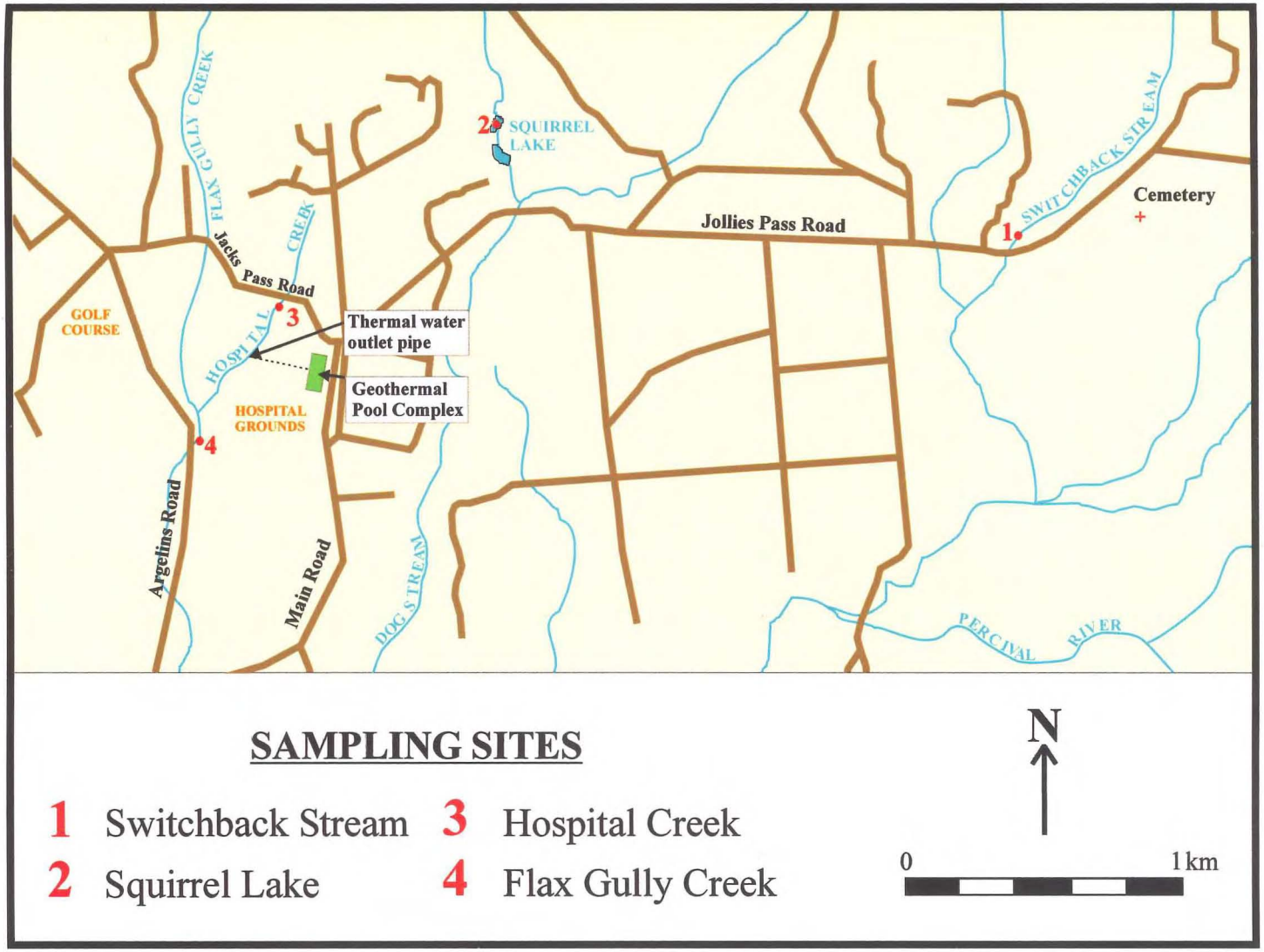


Fig 2.6 Location of study sites around the township of Hanmer Springs.

trees. During spring and summer the site became choked with dense growths of macrophytes, predominantly emergent watercress, *Nasturtium microphyllum,* which is common in ditches and slow flowing streams (Winterbourn & Mason, 1983) (Plates 2.2a & b). In winter, much of this vegetation died off leaving the stream open (Plate 2.2c). Switchback stream was slow flowing and approximately 1 m wide and 30 cm deep at the study site. During periods of increased rainfall water levels sometimes rose significantly and flow became swift (Plate 2.2d). The stream bed consisted of silt and small pebbles on which *P. antipodarum* was abundant. *P. acuta* was absent from this site.

Site 2 - Squirrel Lake

Site 2 was located in Squirrel Lake (Plate 2.3a) which is situated in a clearing surrounded by beech and pine forest, 500 m from the town centre (Fig 2.6). Squirrel Lake is a small eutrophic lake fed by a tributary of Dog Stream and is subject to fluctuating water levels (Plate 2.3b & c) and algal blooms (Plate 2.3d). It is frequented by various waterfowl, predominantly ducks, and the Canadian pond weed *Elodea canadensis* was the dominant submerged macrophyte. Squirrel Lake contained large populations of both *P. antipodarum* and *P. acuta.*

Site 3 - Hospital Creek

Site 3 was located on Hospital Creek, which arises from seepage and runoff from nearby Conical Hill (Fig 2.6). Site 3 was situated about 200 m from the source and was bordered by a variety of exotic trees, especially oaks that provided a major source of leaf litter to the creek (Plate 2.4a). Hospital Creek was approximately 1 m wide and 20 cm deep at the sampling site and was generally slow flowing. However, like Switchback stream, water levels could change rapidly during periods of heavy rainfall and runoff and flow velocity could increase dramatically (Plate 2.4b). Both *P. antipodarum* and *P. acuta* were present at this site.

Site 4 - Flax Gully Creek

Site 4 was located on Flax Gully Creek, 100 m below its confluence with Hospital Creek (Fig 2.6). Site 4 was a geothermally influenced site approximately 300 m downstream from the effluent pipe draining the thermal pools. As a result, Site 4 had elevated water temperature,

Plate 2.2 a) *Site 1* - Switchback Stream, spring growth of dominant macrophyte *Nasturtium microphyllum.*

Plate 2.2 b) Summer growth of riparian vegetation at Switchback Stream.

Plate 2.2 c) Switchback Stream during winter.

Plate 2.2 d) Switchback Stream at high flow.

Plate 2.3 a) *Site 2* - Squirrel Lake.

Plate 2.3 b) Low water level at Squirrel Lake.

Plate 2.3 c) High water level at Squirrel Lake.

Plate 2.3 d) Algal bloom at Squirrel Lake.

Plate 2.4 a) *Site 3* - Hospital Creek.

Plate 2.4 b) Hospital Creek at high flow.

and the stream bed which consisted of silt and large pebbles was coated with a thick algal mat. Riparian vegetation at Site 4 consisted primarily of willow trees and the stream was approximately 1.5 m wide and 40 cm deep (Plate 2.5a). Flow was generally slow, but after high rainfall, water levels could reach the top of the stream bank (Plate 2.5b). Large numbers of *P. antipodarum* occurred at this site but *P. acuta* was absent.

Water Temperature

Electronic temperature loggers (Optic Stowaway®; Onset Corp.) were installed at each study site. The loggers recorded water temperature every hour and were left in place from January to December 1998. Average monthly water temperatures differed at each site (Fig 2.7). The thermally influenced Site 4 on Flax Gully Creek had elevated average monthly water temperatures throughout the year. During the summer, Site 4 had the highest monthly average of 25°C, whereas Site 1 on Switchback Stream had the lowest (15.5°C). Similarly in winter, Site 4 had the highest average monthly temperature (13°C), and Site 1 the lowest (4.9°C). Maximum annual water temperatures differed at each site, but minima were similar at Sites 1, 2 and 3. Site 2 (Squirrel Lake) had the highest summer water temperature of the three and the steepest fall in temperatures during autumn.

Water Chemistry

Water samples were collected from each site monthly from January to December 1998, and pH, conductivity, alkalinity and dissolved oxygen concentration were determined on them. pH, conductivity (at 25°C) and DO were measured with appropriate meters, the latter in the field at mid afternoon each month. Alkalinity was determined by titration with 0.01N HCl (Mackereth, 1963). Water pH was near neutral at all sites, and displayed no obvious seasonal variation (Fig 2.8a). The high pH reading obtained in February (10.2) at Site 2 could have been associated with high levels of photosynthesis within the dense beds of *Elodea canadensis.* Conductivity values for Sites 1, 2 and 3 ranged from 94 to 197 $\mu S\ cm^{-1}$ throughout the year, but the geothermally influenced Site 4 had extremely high conductivity values, the highest being 1743 $\mu S\ cm^{-1}$ (Fig 2.8b). Thermal water of high ion concentration may account for these high conductivity values (Table 2.1), and the variation throughout the year could be due to changes in discharge rates of water from the thermal pools and differing

Plate 2.5 a) *Site 4* - Flax Gully Creek.

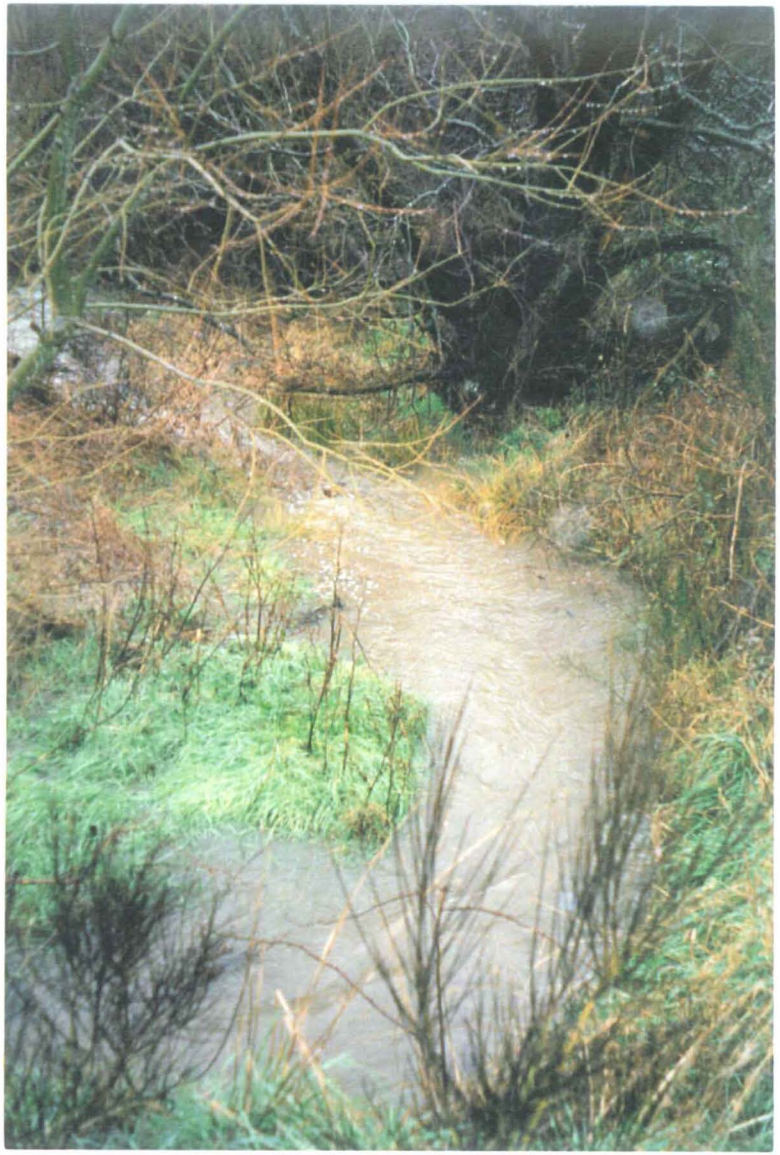


Plate 2.5 b) Flax Gully Creek at high flow.

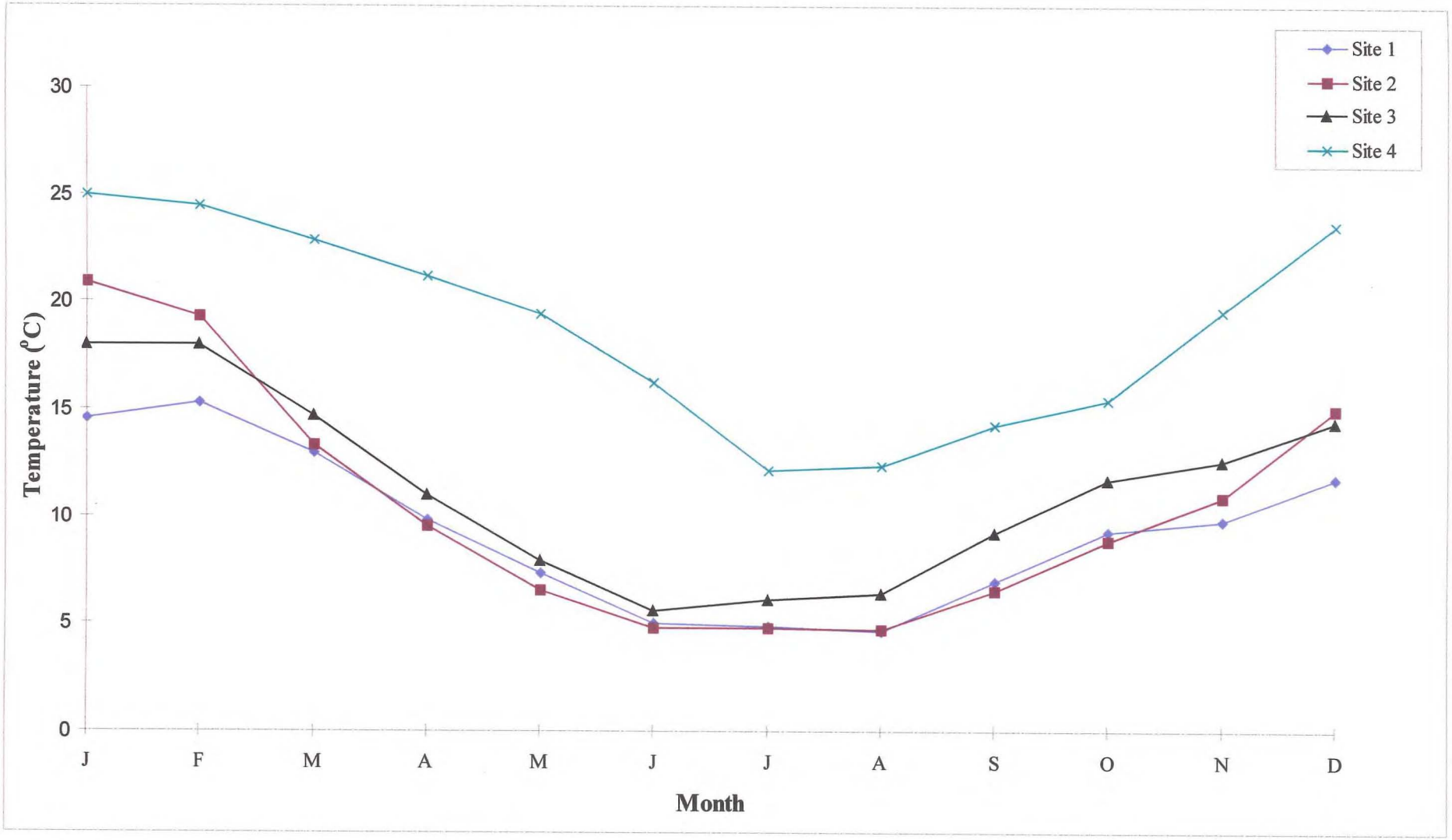


Fig 2.7 Average monthly water temperatures (January - December 1998) at each of the Hanmer Springs sites.

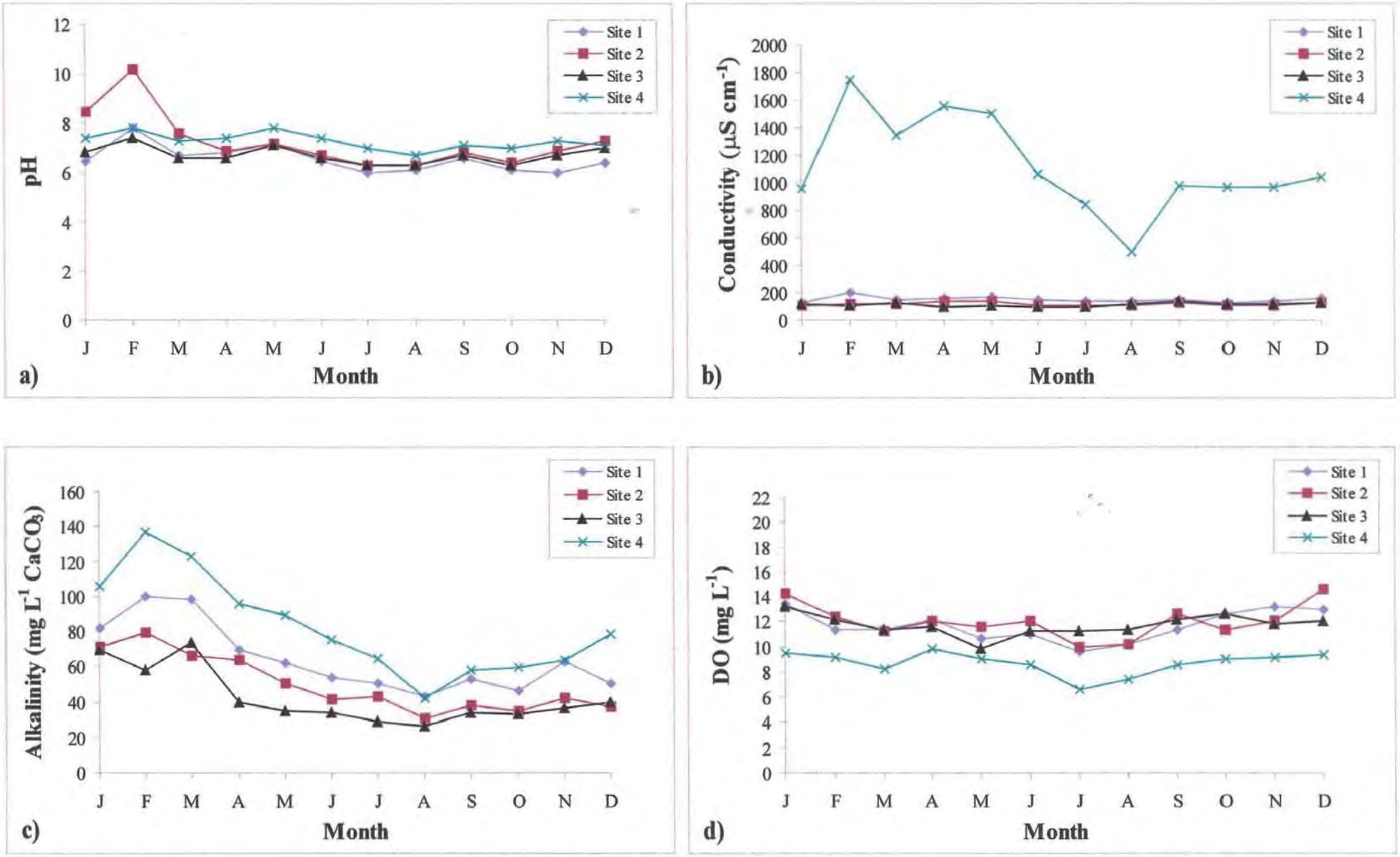


Fig 2.8 Water chemistry results, sampled monthly for each site: **a)** pH, **b)** Conductivity, **c)** Alkalinity, **d)** Dissolved Oxygen (DO).

degrees of dilution by creek water. Alkalinity values were variable between sites and again the highest readings were recorded at Site 4 (Fig 2.8c). There appeared to be a seasonal trend as alkalinity decreased during winter and was lowest in August at all sites. Graesser (1988), found that alkalinity decreased with increasing discharge, therefore decreasing alkalinity values at each site could be attributed to increased rainfall and generally higher flows during winter. Dissolved oxygen (DO) concentration differed between sites and did not appear to show any seasonal variations. At Sites 1, 2 and 3 DO was always greater than 10 mg L^{-1} but values fell as low as 6.8 mg L^{-1} at Site 4. DO is affected by water temperature which determines saturation levels and the elevated water temperatures at this site would have contributed to the low readings.

Table 2.1 Chemical composition of the Hanmer Springs thermal water sampled from the thermal bore head of the well (ESR Analytical Report, 1997).

Chemicals Present	**Concentration (mg L^{-1})**
Fluoride	5.4
Chloride	480*
Bromide	1.5
Sulphate	16
Lithium	1.45
Sodium	350*
Potassium	5.2
Arsenic	<0.002
Reactive Silica (as SiO_2)	43
Boron	53
Calcium	5.5
Magnesium	<0.3
Manganese	<0.02
Iron	<0.1
Bicarbonate	190*

* Note high concentrations of Chloride, Sodium and Bicarbonate.

CHAPTER THREE

EFFECTS OF TEMPERATURE ON THE GROWTH AND REPRODUCTIVE BIOLOGY OF *P. ANTIPODARUM* AND *P. ACUTA.*

Introduction

Over the last 30 years, populations of *P. antipodarum* in Europe and Australasia have been the subject of numerous ecological and distributional studies (Gangloff, 1998). In particular, much of this work has focussed on dispersal mechanisms and factors affecting the establishment of *P. antipodarum* in freshwater systems (Ponder, 1988; Haynes et al. 1985). Both active and passive dispersal methods have contributed to the spread of *P. antipodarum* throughout many European countries and presumably those elsewhere. Because *P. antipodarum* lacks a lung, long range dispersal of snails is limited to transport underwater or in damp media (Gangloff, 1998). *P. antipodarum* like all hydrobiids has an operculum that it can use to seal itself into its shell and avoid unfavourable conditions. The operculum is capable of forming a tight seal and according to Gangloff (1998), snails have been reported to survive out of water for several hours depending on temperature and humidity.

P. antipodarum is well suited for passive dispersal by birds such as waterfowl, most likely adhering to feathers and encrusted mud. However, the rapid spread of the snails within the Madison River watershed in North America, is likely to have been assisted by humans (Anon, 1998). Water users such as anglers, boaties, swimmers and pets could inadvertently also be responsible for interbasin transfer of *P. antipodarum* in North America. Once introduced, *P. antipodarum* can spread quickly in aquatic environments and Haynes et al. (1985), reported that in one instance snails moved 60 m upstream in only 3 months. Bowler (1991), reported that *P. antipodarum* colonised all of Lake Zurich, Switzerland (40 km long) in less than 7 years, with densities of over 100 000 individuals/m^2 occurring in places. Ponder (1988) noted that snail densities in Australia can fluctuate considerably with 50 000 individuals/m^2 during summer months and lows of 1 800 individuals/m^2 in winter. Similarly, Siegismund & Hylleberg (1987) found that *P. antipodarum* in the Kysing Fjord estuary, Denmark reached densities of 50 000 individuals/m^2 in summer. However, when the estuary froze in winter, numbers crashed to nearly zero. Such patterns of fluctuating density indicate that temperature might restrict the dispersal, growth, fecundity and seasonal densities of *P. antipodarum* not only in Europe, but also in North America.

Temperature is one of the most important factors affecting oxygen uptake rates in freshwater snails (Aldridge, 1983; Britton & McMahon, 1998). If oxygen consumption decreases as soon as the oxygen supply diminishes, it is likely to be unfavourable since one or more physiological functions of the organism may then be depressed (Berg & Ockelmann, 1959). Such a reaction may not be so decisive that the organism cannot exist at the locality, but the species may not thrive so well, for example, with respect to growth and extent of egg production, which may be reduced at high temperatures (Berg & Ockelmann, 1959). Hudson (1975) reported that *P. antipodarum* respired at different rates depending on the nature of the locality from which they were taken. As my study included a thermally influenced site, I was interested in comparing the respiratory rates of *P. antipodarum* from different temperature regimes, as high temperatures may limit the geographical distribution of *P. antipodarum*.

In this chapter I report the results of three experiments designed to determine some of the effects of temperature on the growth of *P. antipodarum* and *P. acuta*, and to determine whether differences in reproductive activity occur in the two species. I also describe a laboratory study designed to determine whether respiratory rates of *P. antipodarum* taken from different habitats differ, and to investigate the effect of water temperature on the rate of oxygen consumption. In summary, the work discussed in this chapter was focussed on four questions:

1) Does water temperature affect growth rates of *P. antipodarum* and *P. acuta*?
2) Do the two species differ in reproductive output?
3) Do fecundity levels differ between study sites?
4) Does temperature affect respiration rate and hence possible life history characteristics of *P. antipodarum*?

Feeding Experiment

An appropriate food source for *P. antipodarum* and *P. acuta* was required for laboratory experiments. At Site 2 (Squirrel Lake), both *P. antipodarum* and *P. acuta* were found in abundance on the submerged pond weed *Elodea canadensis*, suggesting that *E. canadensis* may be a desirable food source for both snail species. Winterbourn (1970a) had previously reared *P. antipodarum* in jars containing *E. canadensis* but had not determined whether snails ate the plant.

Most freshwater snails are herbivorous grazers that feed on bacteria, protists and algae as well as fine detritus. A finely toothed radula is used to ingest such materials, which are often described as *Aufwuchs* (Aldridge, 1983). *Aufwuchs* was defined by Russell-Hunter (1978), as the scum flora of diatoms, blue-green and other single celled algae, filamentous algae, bacteria, fungi, protozoans and other associated microscopic plants, all attached to hard surfaces including macrophytic plants (such as *E. canadensis*), rocks, weed and miscellaneous debris.

A preliminary feeding experiment was conducted to determine whether *E. canadensis* would provide a food source for *P. antipodarum* and *P. acuta*. Snails from Site 3 (Hospital Creek) where *E. canadensis* was absent, were used in the experiment.

Ten *P. antipodarum*, and ten *P. acuta* from Site 3 were placed in two 200 ml plastic containers, with 100 ml of tap water, and left for 24 hours to allow gut clearance. Water was changed after 24 hours and 20 cm strands of *E. canadensis* were introduced to each container. Snails were left for 48 hours at ambient air temperature, after which faecal pellets were collected and examined under a compound microscope.

Both *P. antipodarum* and *P. acuta* had grazed on *E. canadensis* and their faecal pellets contained traces of partially digested epidermis of the plant, as well as diatoms (predominantly *Cocconeis* sp.) and the filamentous green alga *Ulothrix*, which were growing on the oxygen weed. Similarly, Stark (1981), found the major food components in faecal pellets of *P. antipodarum* fed on *E. canadensis* were diatoms, followed by macrophyte fragments, detritus and filamentous algae. My observations, combined with Stark's (1981) findings and Winterbourn's (1970a) successful use of oxygen weed in rearing containers, suggested that *E. canadensis* would provide an appropriate food source. It was therefore used in all laboratory experiments.

Experiment 1

Effects of temperature on the growth of *P. antipodarum* and *P. acuta*

Methods

Collections of snails were made monthly from March to July 1998. Each site was sampled by sweeping the sediment and macrophytes with a long-handled, triangular dip net. The snails were transported back to the laboratory in plastic bags containing water from the locality. Because *P. antipodarum* reaches sexual maturity at a shell height of approximately 3.5 mm (Lassen, 1979), juvenile snails (shell height (s.h.)< 3.5 mm) were chosen for experimental work to ensure there would be visible shell growth in the laboratory. Likewise, only juvenile *P. acuta* (s.h.< 6 mm) (Krkac, 1982) were used.

The trials described below were repeated on five occasions starting each month from March to July 1998. Ten juvenile *P. antipodarum* from each site (1 to 4), and ten juvenile *P. acuta* from Sites 2 and 3 were randomly selected and their shell heights were recorded to 0.1 mm with an eye piece graticule fitted in a stereoscopic microscope.

The ten snails from each site were placed together in 200 ml plastic containers filled with 100 ml of tap water. To help maintain aeration of the water throughout the experiment and to provide a food source, 20 cm strands of *E. canadensis* were placed in each container. This procedure was repeated until each site was represented by three containers with ten juvenile *P. antipodarum*. Because *P. acuta* occurred only at Sites 2 and 3, triplicate containers were set up for these sites. The containers were kept in three temperature control rooms (4, 8 and 15°C with a 12:12 hour light/dark cycle) (Fig 3.1).

Snails were left to grow at each of the three temperatures for 15 weeks, during which water and *E. canadensis* were changed weekly. Dead snails were removed and replaced with identical sized individuals from the same locality. Shell height was measured and recorded every five weeks. Each 15 week experiment was carried out in five successive months (March to July 1998).

Growth data were checked for normality and log-transformed when necessary before being analysed statistically for differences between temperature and month using a parametric one-way ANOVA (α=0.05; Zar, 1984). A Tukey multiple comparison *a posteriori* test was used to determine where significant differences occurred among treatments.

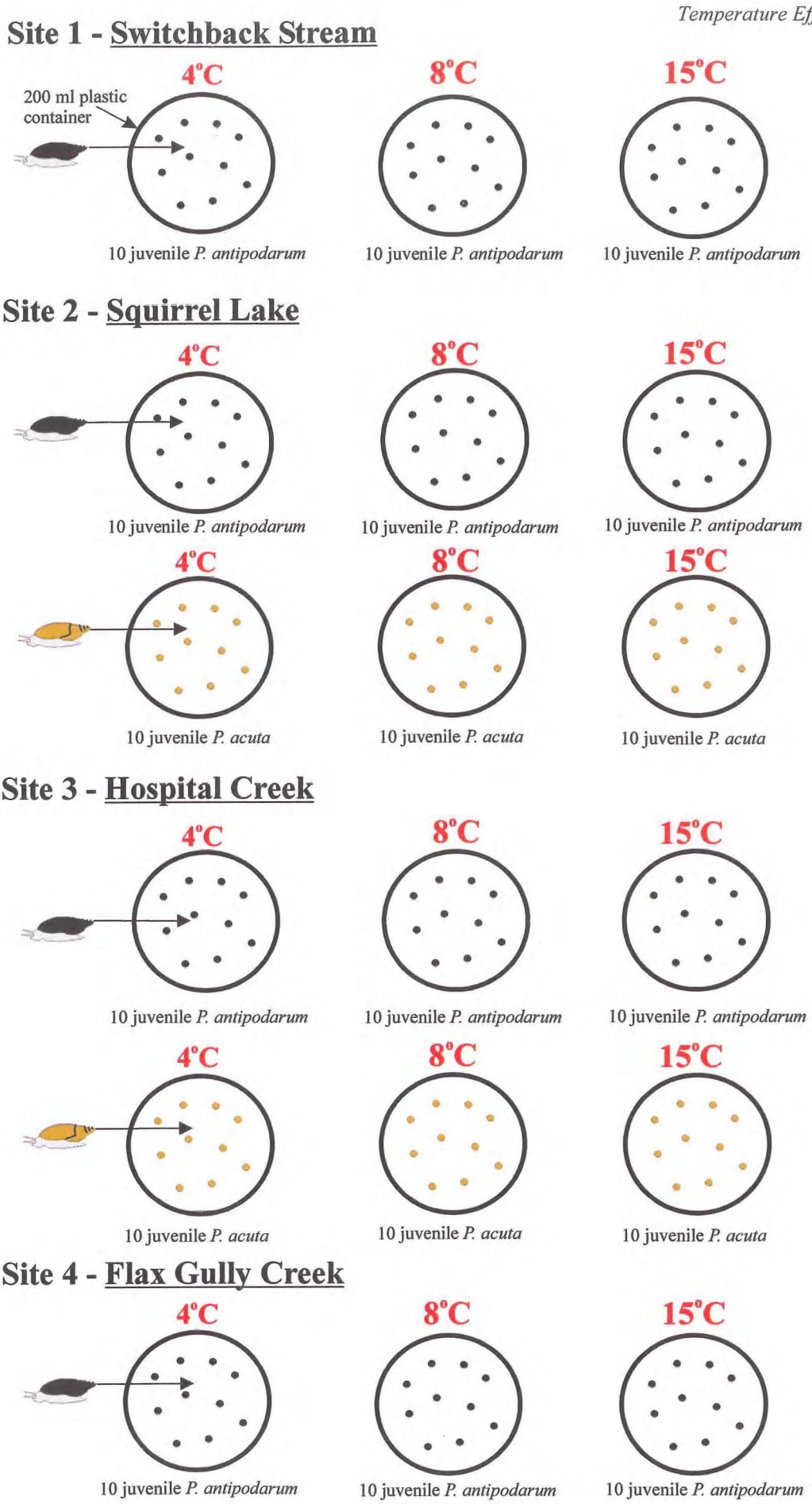


Fig 3.1 Experimental set up for the study of growth in *P. antipodarum* and *P. acuta*. Six containers were kept in each of 4, 8 and 15°C temperature control rooms.

Results

Mean shell growth rates after 15 weeks (for both *P. antipodarum* and *P. acuta*) at 4, 8 and 15°C are shown in Figure 3.2. Mean individual growth ranged from 0.27 mm in trials established in May to 1.81 mm for those begun in March. Growth rates differed significantly with temperature ($P<0.0001$) being lowest at 4°C and highest at 15°C, a trend that was consistent in all months (Fig 3.2).

Snail growth also differed significantly between months ($P<0.0001$). In the 15 weeks following March, growth rates at 8 and 15°C reached their maxima and then decreased to lows in May (0.47 mm) and June (0.89 mm), respectively. A Tukey test indicated that snail growth in March did not differ from that in April, but was significantly greater than growth in May, June and July. Shell growth at 4°C was maximal for snails collected in April (0.74 mm/15 weeks). Growth declined considerably in May (0.27 mm) and increased again in the weeks following June and July. Overall, growth patterns were not significantly different in May, June and July.

Site differences were determined for mean growth of *P. antipodarum* and *P. acuta* at 4, 8 and 15°C (Fig 3.3a & b). Growth at each site was again lowest at 4°C and highest at 15°C for both species. Growth rates differed significantly at different temperatures and among sites for *P. antipodarum* ($P<0.0001$ and $P=0.011$, respectively) (Fig 3.3a). However, Tukey tests indicated that shell growth was not significantly different at Sites 1, 2 and 3, but was significantly slower at Site 4 than at Sites 2 and 3 (Table 3.1). Snails from the thermally influenced Site 4 grew three to four times more at 15°C than at 4 or 8°C, but overall shell growth at Site 4, was not significantly different from that achieved by Site 1 snails (Table 3.1). *P. antipodarum* from Site 3 had the greatest mean shell growth at 4 and 8°C, whereas *P. antipodarum* from the thermally influenced Site 4 grew very little at these cooler temperatures (0.21 and 0.33 mm, respectively) (Fig 3.3a).

In contrast to *P. antipodarum*, growth rates of *P. acuta* from Sites 2 and 3 did not differ ($P>0.05$) and snails reared at 15°C, grew at rates similar to those raised at 8 and 4°C ($P>0.05$) (Fig 3.3b).

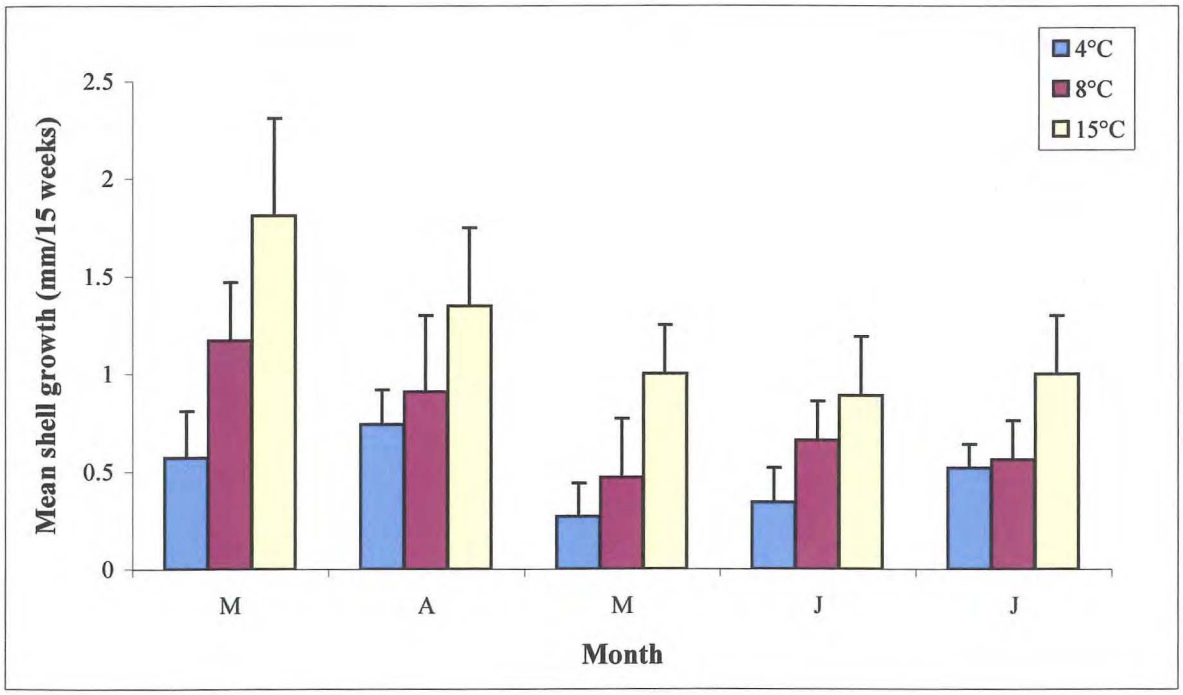


Fig 3.2 Mean growth (mm height increase ± 1SE) of *P. antipodarum* and *P. acuta* after 15 weeks at 4, 8 and 15°C. Results of five trials starting each month from March to July are shown. Snails from field populations combined.

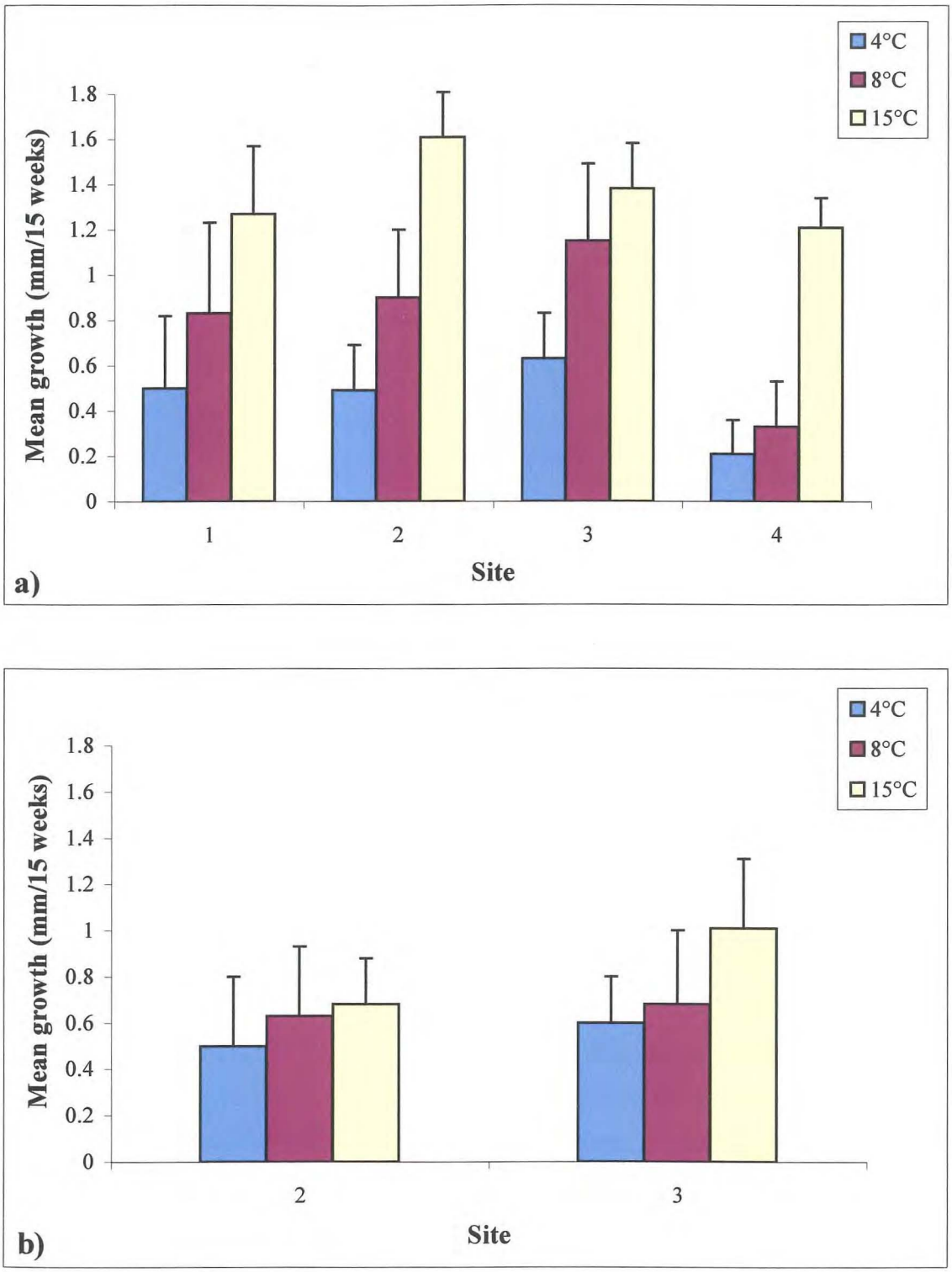


Fig 3.3 Mean shell growth (mm height increase ± 1SE) after 15 weeks in the five monthly laboratory trials with snails from each site at three temperatures. **a)** *P. antipodarum* ; **b)** *P. acuta.*

Table 3.1 Results of a Tukey multiple comparison test showing where significant differences in growth of *P. antipodarum* occurred among field populations.

Site	Homogeneous Groups
3	I
2	I
1	I I
4	. . I

Temporal differences (March to July) in mean growth of *P. antipodarum* and *P. acuta* were also found in the laboratory (Fig 3.4a, b & c). Growth of both species was low at 4°C with maximum growth of *P. acuta* being shown by March-collected snails (0.77 mm/15 weeks), and of *P. antipodarum* by April-collected snails (0.77 mm) (Fig 3.4a). Although the growth rate of *P. acuta* was higher than that of *P. antipodarum* in four of the five monthly experiments at 4°C, no significant difference in growth were found between the two species ($P>0.05$). Similarly, there were no significant differences in mean shell growth of *P. antipodarum* and *P. acuta* between months ($P=0.09$ and $P=0.16$, respectively).

Growth rates at 8°C did not differ significantly between *P. antipodarum* and *P. acuta* ($P>0.05$) and no significant differences in mean growth were observed between months for *P. antipodarum* (Fig 3.4b). Although a significant difference in mean growth of *P. acuta* occurred between months ($P<0.01$) a Tukey test indicated that the only significant difference was between March and May. Both species had their maximum growth rates in March.

Similarly, maximum growth of *P. antipodarum* and *P. acuta* raised at 15°C was found in March (Fig 3.4c). Overall, shell growth of both species was highest at this warmer temperature and was significantly greater in July for *P. antipodarum* than *P. acuta* ($P<0.05$). The mean growth among months was significantly different for *P. antipodarum* ($P=0.02$) with a Tukey test indicating shell growth in March was significantly greater than in July. Growth in March was significantly greater than growth in June for *P. acuta* ($P<0.01$), and growth rates for both species declined following March.

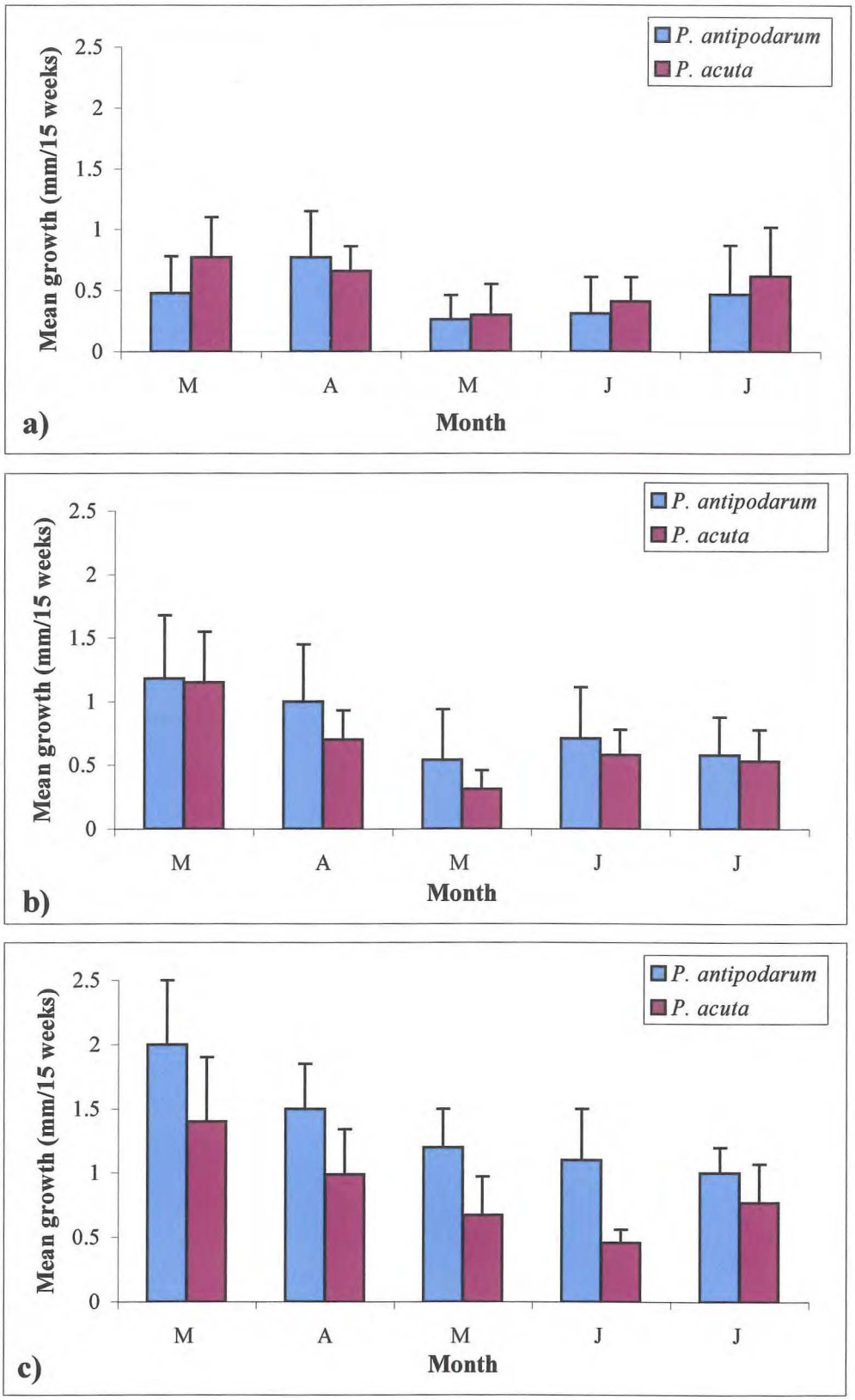


Fig 3.4 Mean shell growth (mm height increase ± 1SE) of *P. antipodarum* and *P. acuta* after 15 weeks in the five monthly laboratory trials at **a)** 4°C, **b)** 8°C and **c)** 15°C. Snails from all field populations combined.

REPRODUCTIVE BIOLOGY OF *P. ANTIPODARUM* AND *P. ACUTA*

1. Reproductive condition of field collected *P. antipodarum*

Methods

Observations on the numbers of young present within the brood pouch of *P. antipodarum* at the time of collection were made each month from January to December 1998. Snails were collected from Sites 1 to 4 and transported back to the laboratory where 20 adult *P. antipodarum* (s.h.>3.5 mm) were randomly selected from each collection and preserved in 95% methylated spirits.

Preserved snails were removed from their shells by gently cracking them between two glass slides, sexed, and if female, the brood pouch was opened (Fig 3.5) and the numbers of developing eggs and embryos were counted. The presence of parasites was also noted. *P. antipodarum* serves as an intermediate host (Fig 3.6) to at least 14 species of digenetic trematodes, the most common being the metacercariae of *Microphallus* sp. (Jokela & Lively, 1995b). All 14 species appear to castrate both sexes of adult *P. antipodarum* (Winterbourn, 1974).

Data were analysed statistically for differences in the number of embryos present in brood pouches between sites and months using a non-parametric Kruskal-Wallis test (α=0.05; Zar, 1984). A Dunn's multiple comparison *a posteriori* test was used to determine where significant differences occurred among sites.

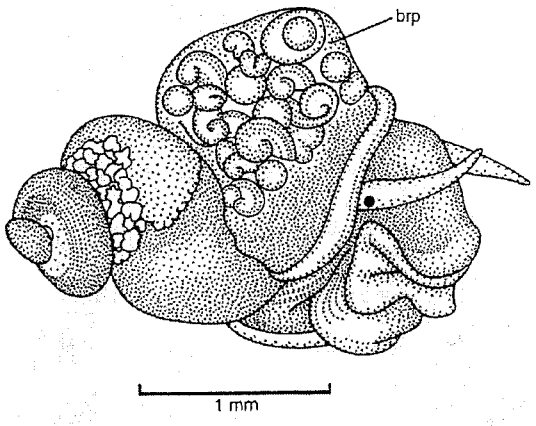


Fig 3.5 *P. antipodarum*, with shell removed, showing unfertilised eggs which develop into young snails inside the brood pouch, formed from the distal pallial oviduct. **brp,** brood pouch (from Fretter et al. 1998).

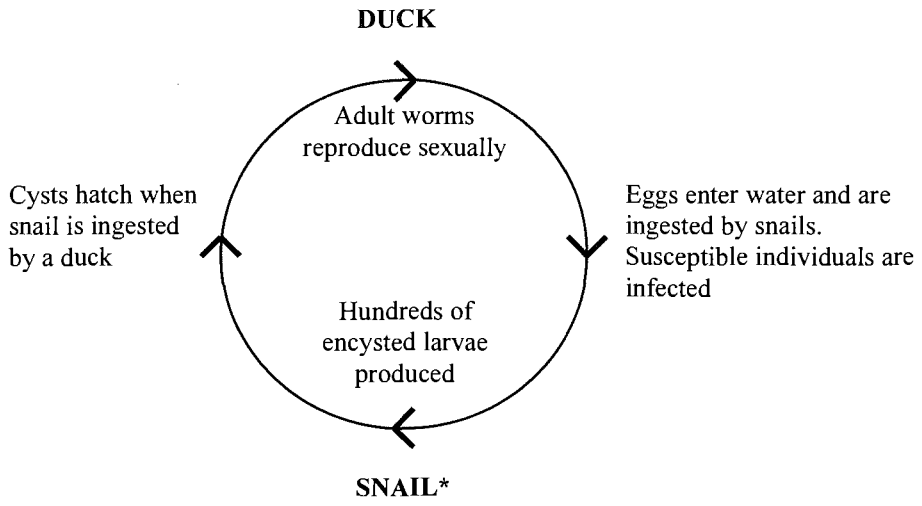


Fig 3.6 Life cycle of the digenetic trematode, *Microphallus* sp. Eggs are produced sexually by the hermaphroditic adult worms, and subsequently are ingested by snails. Successful infections resulting from a single egg sterilise the snail during the production of several hundred blastocercariae, which later become encysted metacercariae. The metacercariae hatch following ingestion by the final host, and mature in about 24 hours (after Lively & Jokela, 1996).

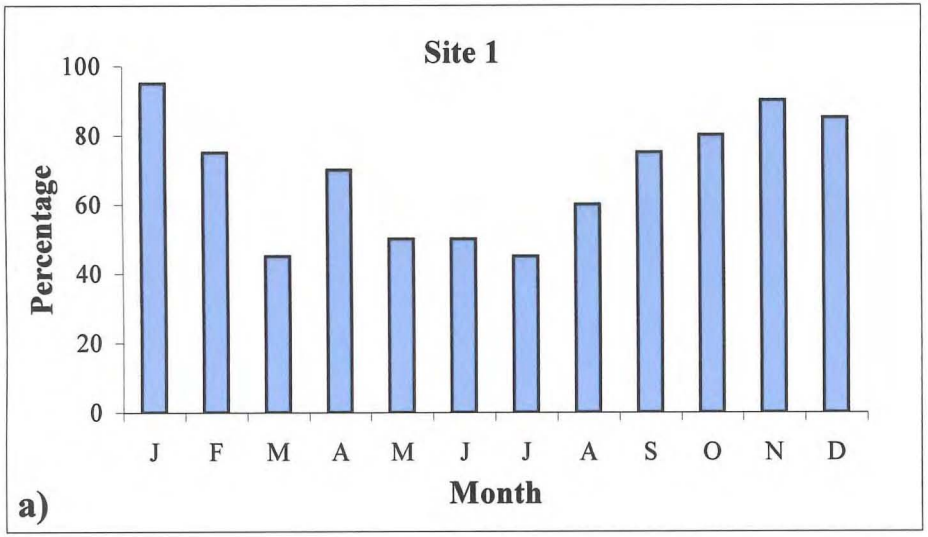
Results

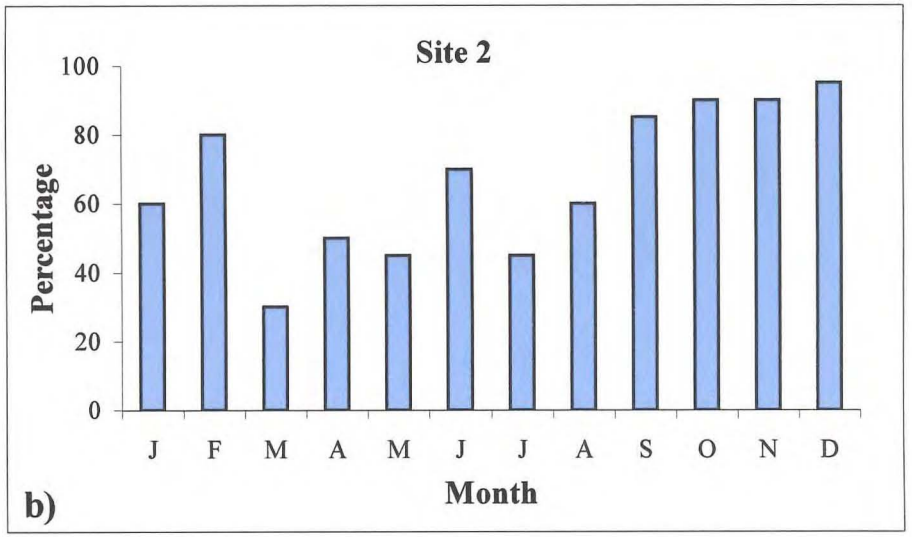
Sites 1, 3 and 4 consisted solely of parthenogenetic females, however, three males were located at Site 2 (Squirrel Lake), one in each of February, March and September.

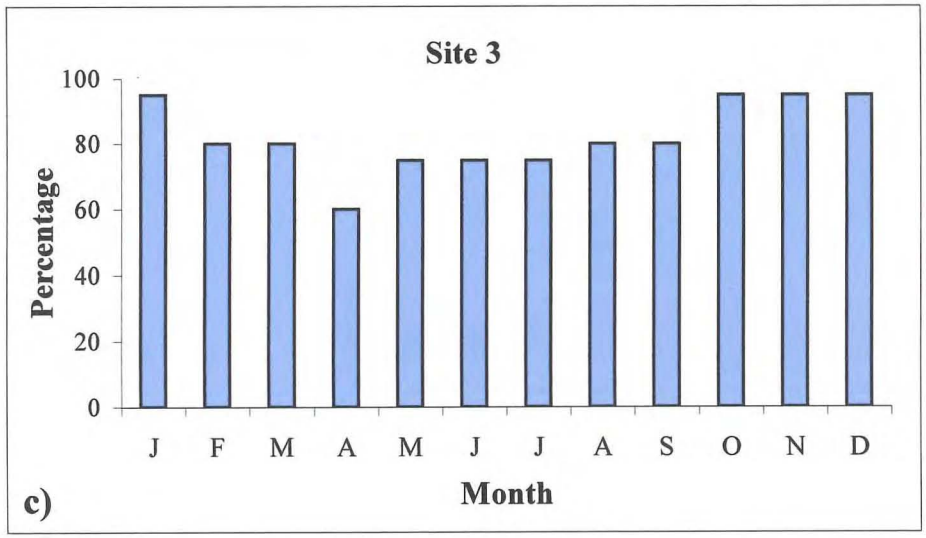
Percentages of reproductively active adult snails found at Sites 1 to 4 are shown in Figure 3.7. At each site, young were found in the brood pouches of snails in all months. Thirty to 95% of snails from Sites 1, 2 and 3 contained young each month, but as few as 5% of adult snails carried embryos at the thermally influenced Site 4 in late summer. At Site 3, the percentage of snails containing embryos did not vary greatly at different times of the year (60 to 95%) and almost all snails examined in late spring and summer carried embryos (Fig 3.7).

At each site, spring and early summer were the times of greatest reproductive activity and the maximum numbers of embryos per snail were also recorded then (September to December 1998) (Fig 3.8).

The mean number of embryos per snail differed significantly between months at each site ($P<0.0001$) (Fig 3.8), but were generally lowest in late autumn and winter (May to August







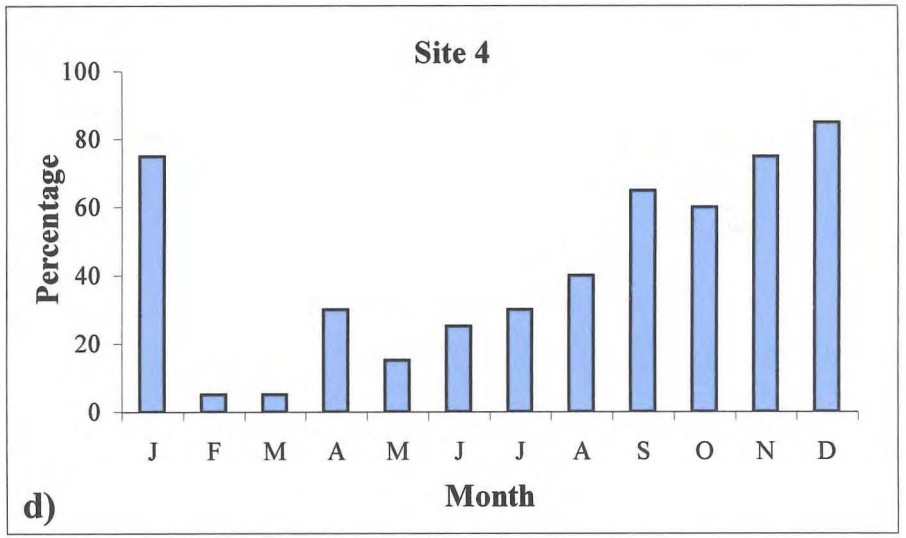


Fig 3.7 Percentage of adult *P. antipodarum* (shell height >3.5 mm) containing embryos each month in four populations; **a)** Site 1, **b)** Site 2, **c)** Site 3 and **d)** Site 4. (n = 20 snails per site per month).

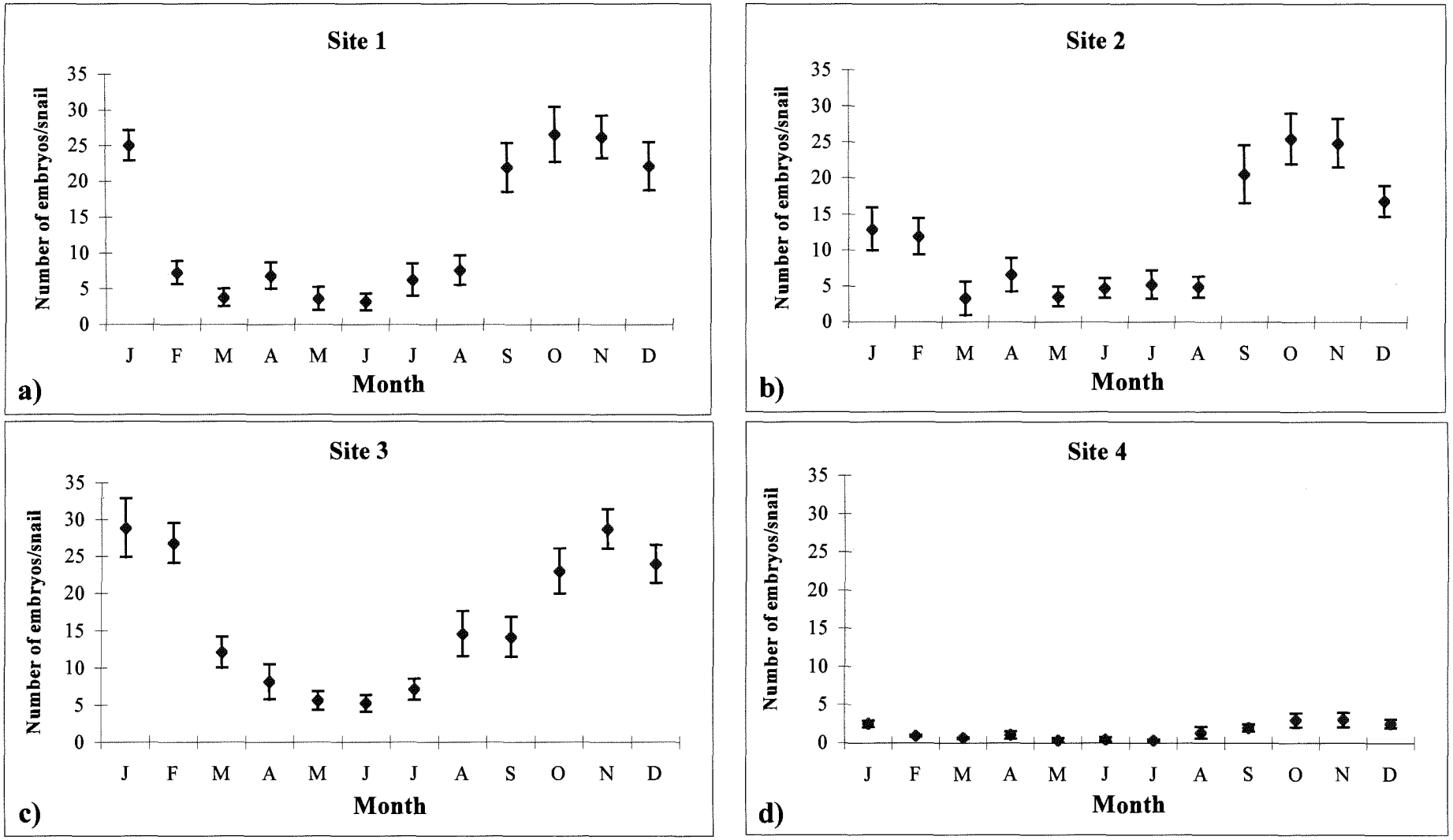


Fig 3.8 Numbers of embryos (mean ± 1SE) found in brood pouches of reproductively active *P. antipodarum* each month at **a)** Site 1, **b)** Site 2, **c)** Site 3 and **d)** Site 4.

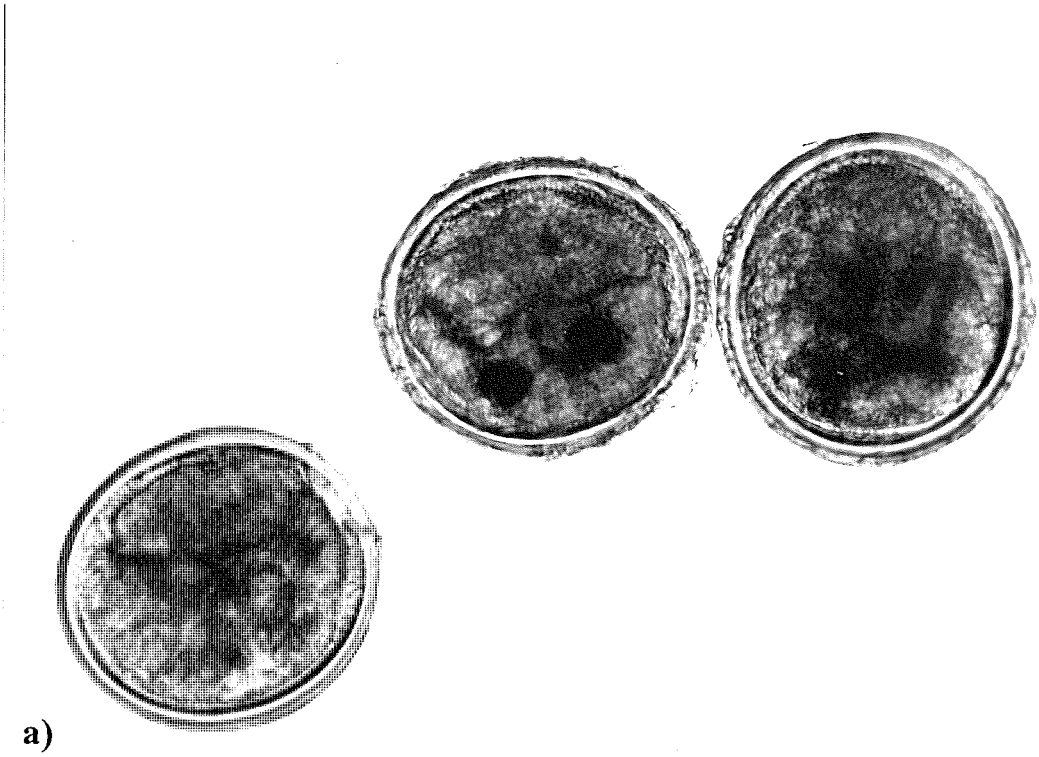
1998). When numbers of embryos per snail were compared among sites, significant differences were also found (P<0.0001). A Dunn's multiple comparison test indicated that Sites 1, 2 and 3 were similar in this respect but differed from Site 4 (Table 3.2). Throughout the year, few embryos were located in snails collected from this thermally influenced Site 4 (monthly range, 0.4 to 3.1 embryos per individual) (Fig 3.8d). Furthermore, the maximum number of embryos found inside one individual from Site 4, was 17, the lowest of the four sites (Table 3.3).

Metacercariae of the trematode *Microphallus* sp. (Plate 3.1a) and a gymnocephalous cercaria (G1) (Winterbourn, 1974) (Plate 3.1b) were located during dissections of snails from Sites 1, 2 and 3. A total of 4.6 % of dissected snails were parasitised by these trematodes, although none were observed at Site 4.

Throughout the year, the greatest proportion of parasitised individuals was observed at Site 1 (15%), compared with 6.3% at Site 2 and 1.7% at Site 3. Sites 1 and 2 were infested with both parasitic species, although *Microphallus* sp. was dominant (Fig 3.9). Only gymnocephalous (G1) cercariae were located at Site 3. The percentage of parasitised individuals varied throughout the year (all three sites combined), with highest infestations in June, July and September (Fig 3.10).

Table 3.2 Results of a Dunn's multiple comparison test showing where significant differences occurred in the number of embryos within brood pouches of *P. antipodarum* in the four field populations. Significant values are shown in bold (P<0.05).

Site	P-value	Summary
Site 1 vs Site 2	P>0.05	ns
Site 1 vs Site 3	P>0.05	ns
Site 1 vs Site 4	**P<0.001**	***
Site 2 vs Site 3	P>0.05	ns
Site 2 vs Site 4	**P<0.01**	**
Site 3 vs Site 4	**P<0.001**	***



a)

b)

Plate 3.1 Trematode parasites **a)** *Microphallus* metacercariae and **b)** a gymnocephalous cercaria, found inside *P. antipodarum* at Sites 1 to 3.

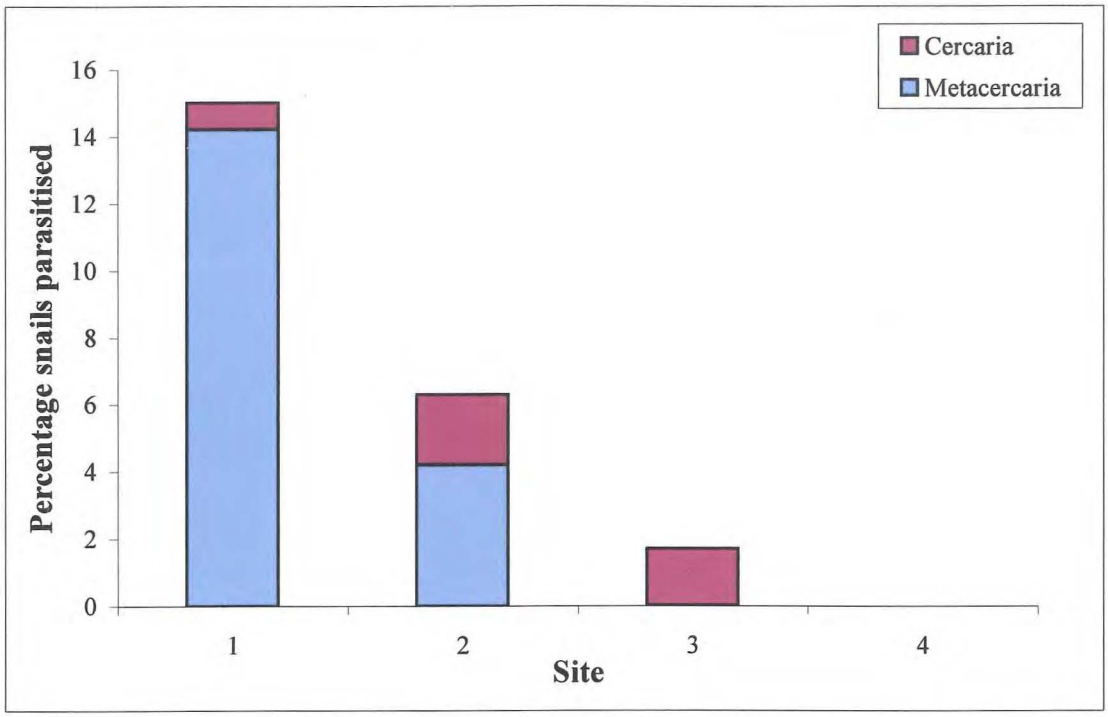


Fig 3.9 Percentage of adult *P. antipodarum* (shell height > 3.5 mm) containing larval trematodes (either *Microphallus* metacercariae and/or a gymnocephalous cercaria), at each site in all months combined.

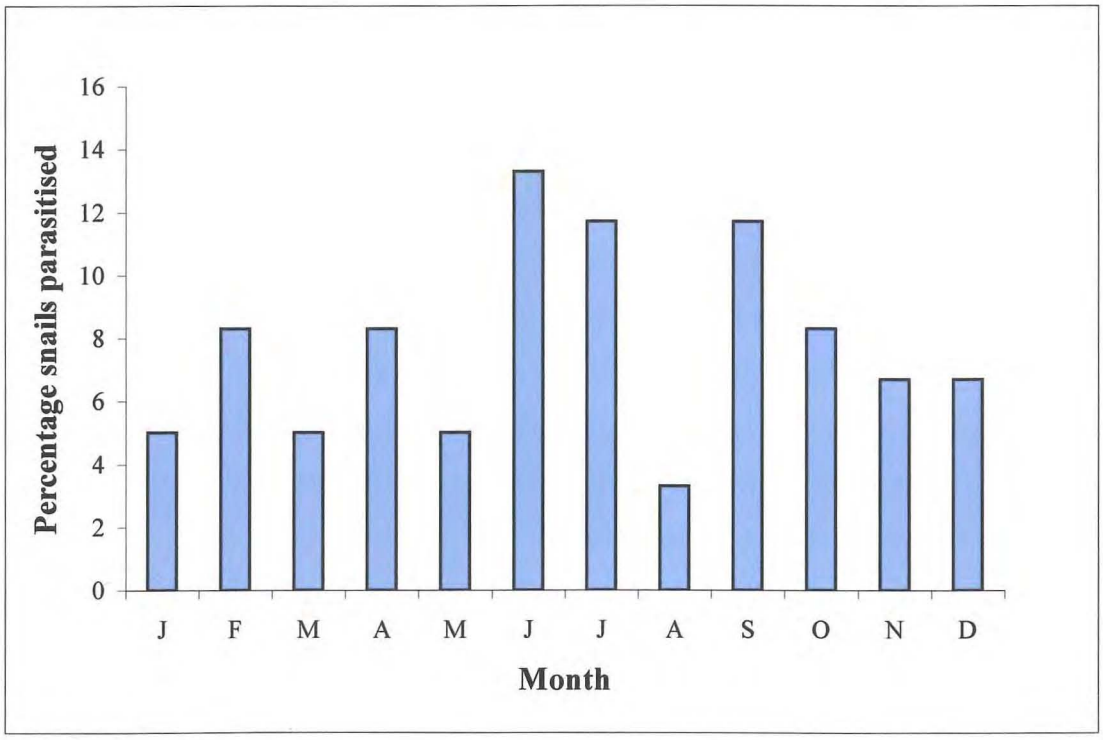


Fig 3.10 Percentage of adult *P. antipodarum* (shell height > 3.5 mm) infested with larval trematodes each month. All sites combined.

Table 3.3 Maximum numbers of embryos found within brood pouches of *P. antipodarum* individuals from the four field populations.

Site	Number of embryos
1	53
2	52
3	74
4	17

Experiment 2

2. Reproductive activity of *P. antipodarum* and *P. acuta*

Methods

P. antipodarum is a viviparous snail whose populations may be entirely parthenogenetic, or include varying proportions of sexually functional males (Zaranko et al. 1997). Wallace (1985), reported that males usually made up less than 5% of populations in the Waikato region, but Winterbourn (1970a) and Lively (1987) reported that up to 40 and 50% of snails were males in some New Zealand lakes and streams. I found three males in the 960 snails dissected from Sites 1 to 4, all from Site 2, Squirrel Lake. Therefore, *P. antipodarum* used in the following experiment were almost certainly parthenogenetically reproducing females.

In contrast to *P. antipodarum*, *P. acuta* is hermaphroditic and embryonic development takes place outside the animal in gelatinous egg masses (Plate 3.2).

Collections of snails were made monthly from February to July 1998. As in Experiment 1, each site was sampled by sweeping the sediment and macrophytes with a long-handled, triangular dip net, and snails were transported back to the laboratory in water from the collection site. Adult *P. antipodarum* (s.h. 3.5-4.0 mm) and *P. acuta* (s.h.=7.0 mm) were selected for experimental work in the laboratory.

The trials described below were repeated on six occasions starting each month from February to July 1998.

Ten adult *P. antipodarum* from Sites 1 to 4 and ten adult *P. acuta* from Sites 2 and 3

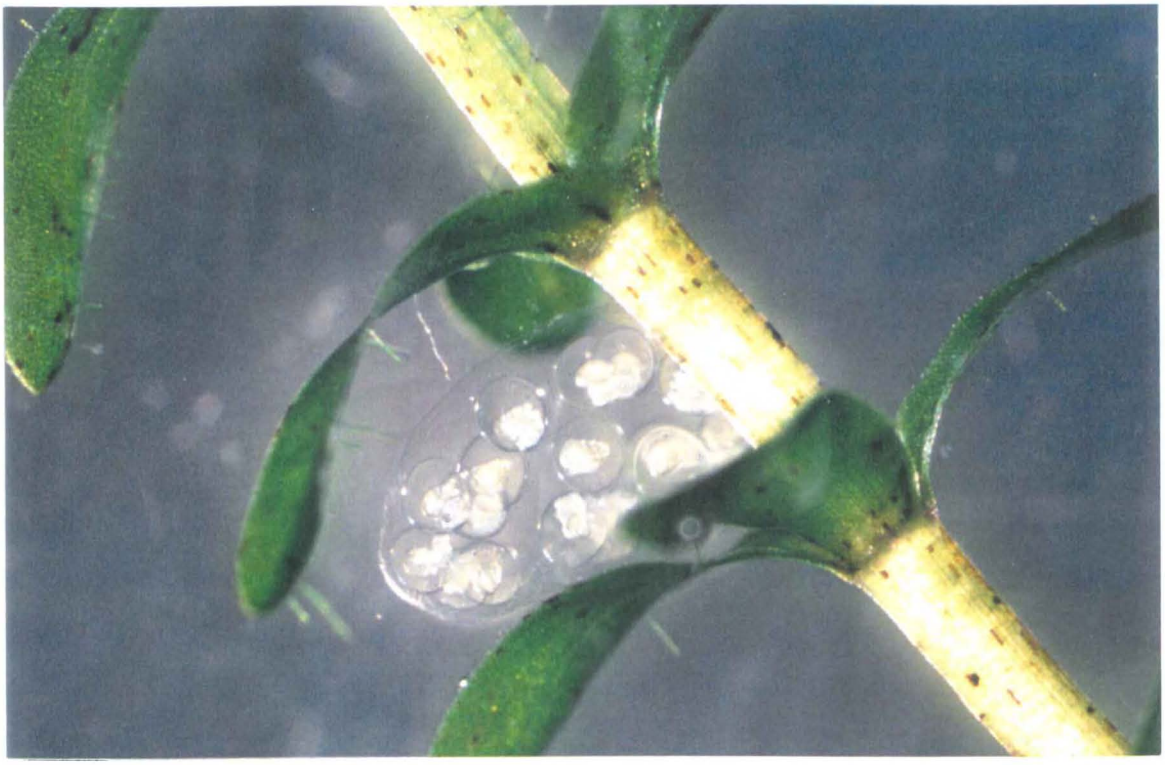


Plate 3.2 Egg mass of *P. acuta* attached to a strand of *E. canadensis*, showing developing embryos.

were set up in separate 200 ml plastic containers (one container per species per site) filled with 100 ml of tap water and one 20 cm strand of *E. canadensis*. The containers were held in a 15°C temperature control room (12:12 hour light/dark cycle) (Fig 3.11), for eight weeks, during which time water and *E. canadensis* were changed weekly. Water and *E. canadensis* were examined under a stereoscopic microscope before discarding them to ensure that newly released snails or egg masses were not lost. Dead snails were removed and replaced with identical sized individuals from the same locality.

Released embryos from gravid *P. antipodarum* and hatched young from the egg masses of *P. acuta* were counted, recorded and removed every two weeks. Each eight week experiment was carried out in six successive months (February to July 1998).

Reproductive output of the two species was compared statistically for differences among sites and months using ANOVA and Tukey tests as described for Experiment 1.

Results

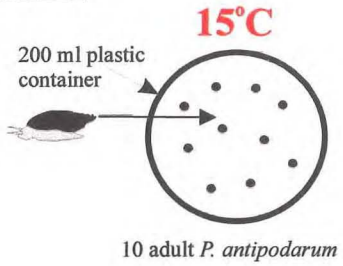
a) *P. antipodarum*

Mean numbers of embryos released in eight weeks from brood pouches of *P. antipodarum* ranged from 24.2 to 0.2 embryos per individual/eight weeks, and differed significantly among sites in the eight weeks following February, April, May and June ($P=0.002$, 0.032, <0.0001 and 0.006 respectively) (Fig 3.12). *P. antipodarum* from Site 3 consistently released the greatest numbers of young, with most being produced by February-collected snails and fewest by June-collected snails (24.2 and 8.2 embryos per individual/eight weeks, respectively) (Fig 3.12a & e). In contrast, snails from the thermally influenced Site 4 released the fewest embryos in all eight week trials (Fig 3.12b & d).

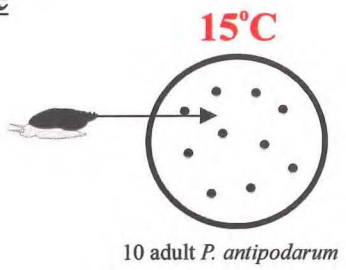
Mean numbers of young released by *P. antipodarum* at each site in all monthly trials combined, differed significantly ($P<0.0001$) (Fig 3.13) and a Tukey test indicated that snails from Sites 1, 2 and 3 had fecundity levels significantly higher from snails at Site 4. Numbers of embryos released by snails from Site 3 were also significantly greater than those from Site 1.

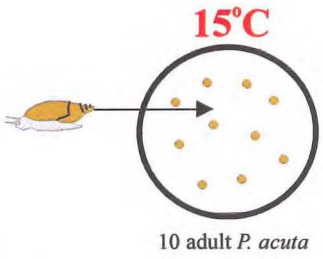
When sites were considered individually, differences in the numbers of embryos released each month were observed only at Site 2 (Table 3.4).

Site 1 - Switchback Stream

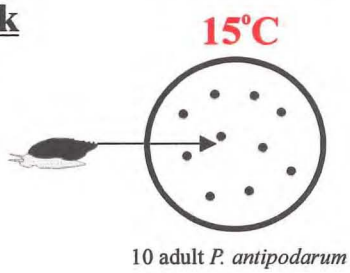


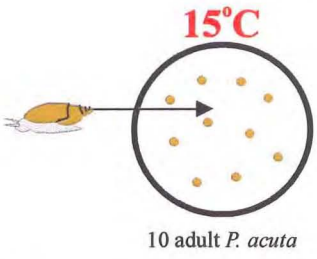
Site 2 - Squirrel Lake





Site 3 - Hospital Creek





Site 4 - Flax Gully Creek

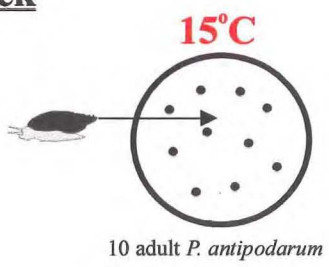


Fig 3.11 Experimental set up for the reproductive study of *P. antipodarum* and *P. acuta*. Six containers were kept in a 15°C temperature control room.

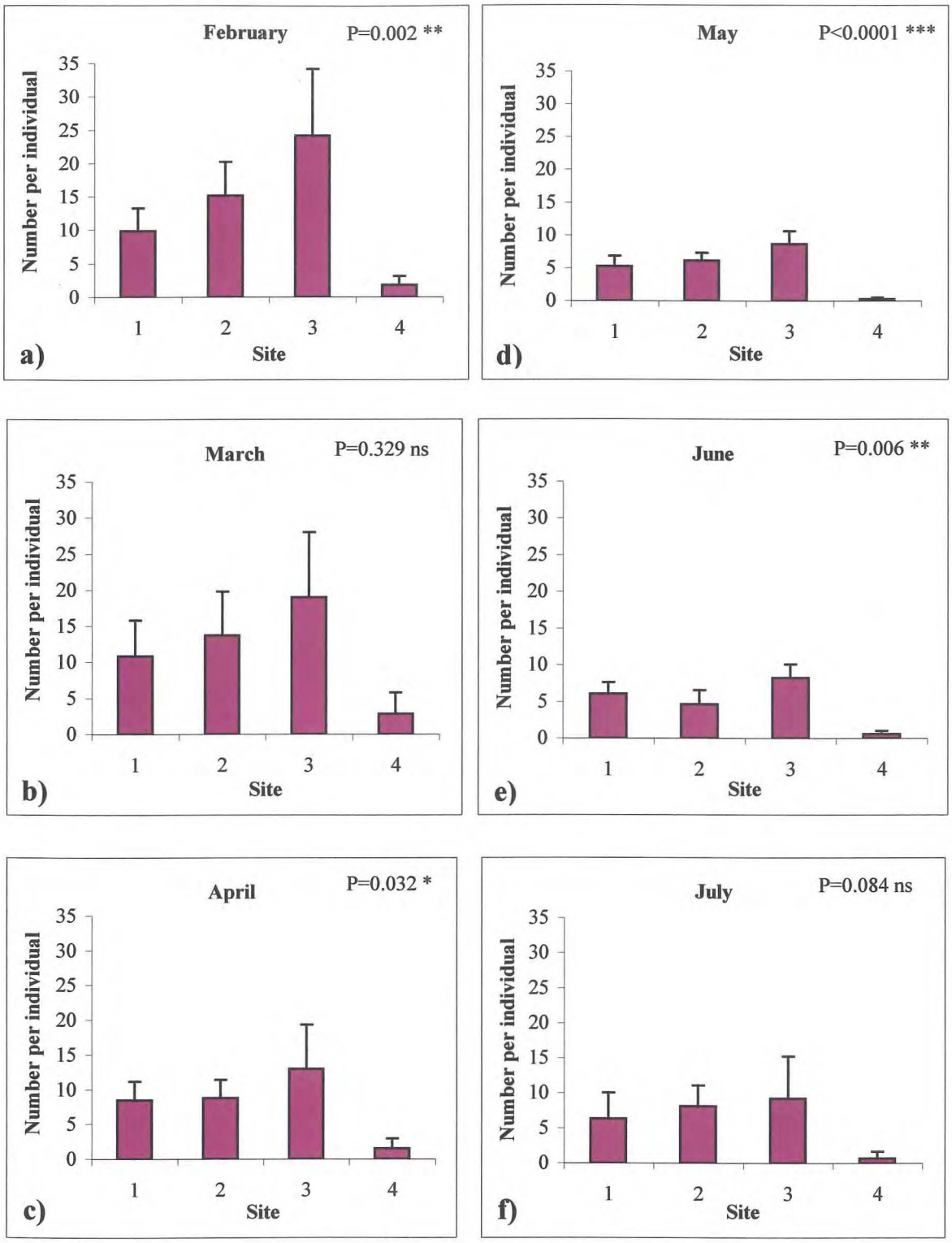


Fig 3.12 Number of embryos released (mean ± 1SE) after eight weeks in the laboratory by *P. antipodarum* from each site in six months.

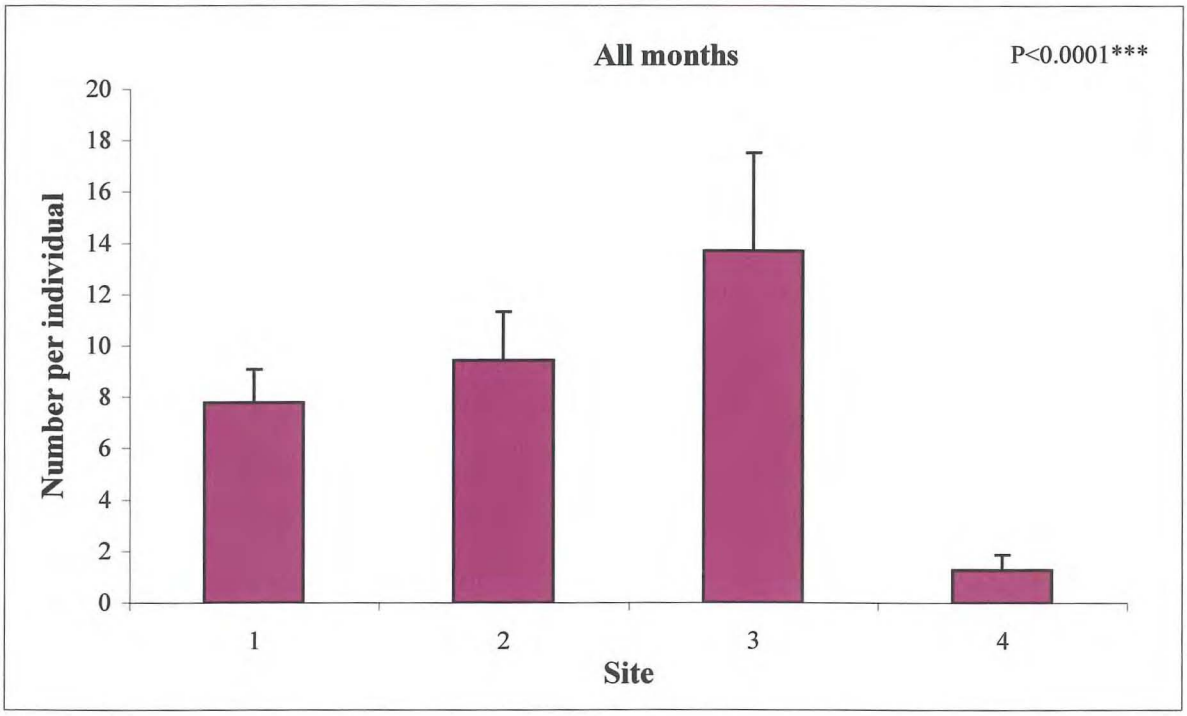


Fig 3.13 Numbers of embryos released (mean ± 1SE) by *P. antipodarum* from each site after eight weeks. All months combined.

Table 3.4 Summary of one-way ANOVAs, comparing mean numbers of embryos released (*P. antipodarum*) and mean numbers of hatched young (*P. acuta*) produced each month at each site (February to July 1998). Significant values are shown in bold (P<0.05).
* = P<0.05, ** = P<0.01, *** = P<0.0001, ns = P>0.05.

Monthly comparison of:	**Site**	**P-value**	**Summary**
Mean number of embryos released by *P. antipodarum*	1	0.2648	ns
	2	**0.0193**	*
	3	0.6801	ns
	4	0.4340	ns
Mean number of young hatched from eggs of *P. acuta*	1	-	-
	2	**<0.0001**	***
	3	**0.0030**	**
	4	-	-

b) *P. acuta*

P. acuta from both Sites 2 and 3 showed significant differences in the mean numbers of young that hatched from eggs during the six month study (Table 3.4). Numbers were greatest in the eight weeks following March (6.6 and 5.8 young per snail/eight weeks), and then declined to reach a low in July (0.5 and 0.4 young per snail/eight weeks) (Fig 3.14). No significant differences were found between sites in the number of young leaving egg masses (P>0.05), however, for both sites, significant differences occurred in the monthly trials, with numbers of young hatched in May, June and July being significantly lower than those in February and March (P<0.001).

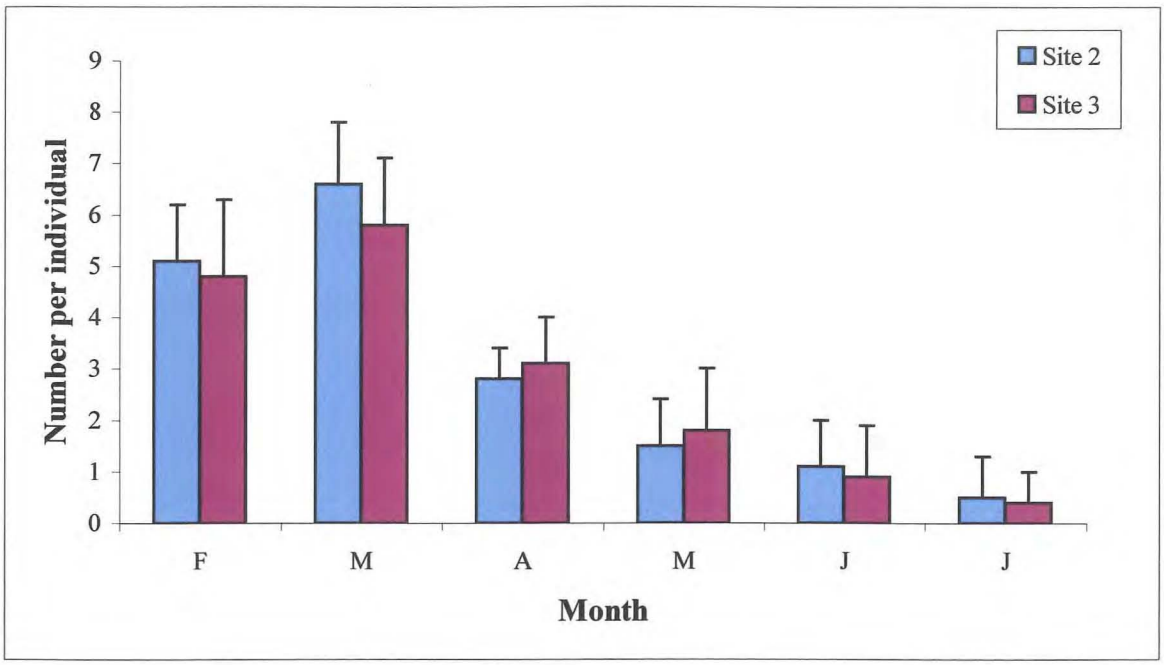


Fig 3.14 Numbers of young released from egg masses (mean ± 1SE) of *P. acuta* taken from Sites 1 and 2 in eight week trials starting each month from February to July 1998.

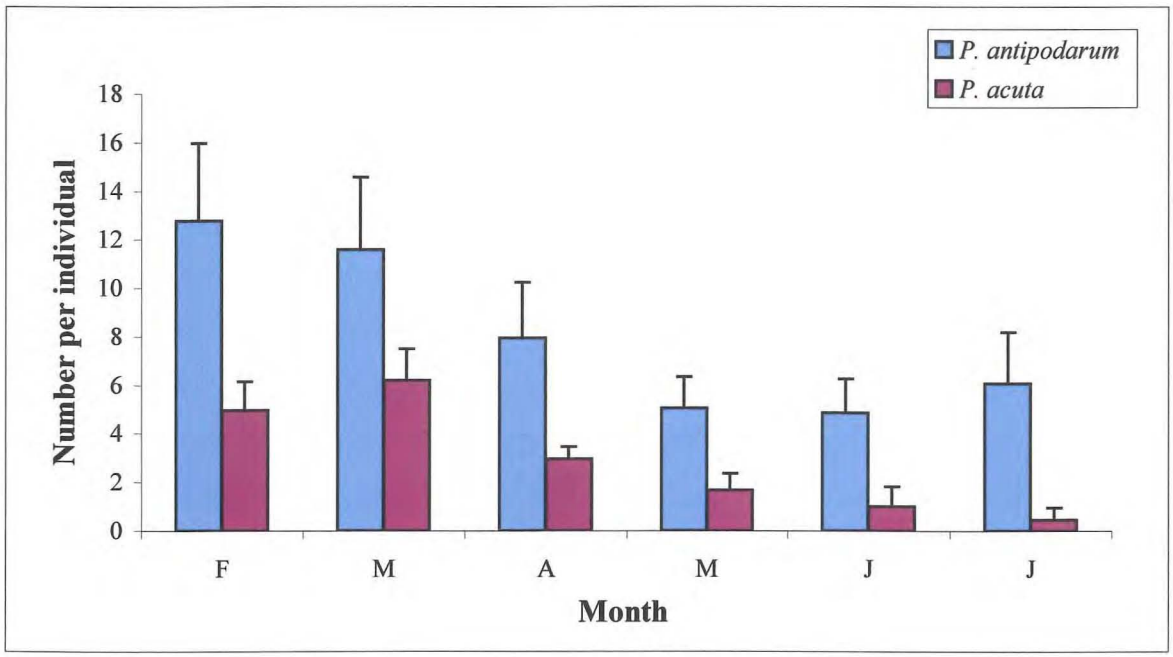


Fig 3.15 Numbers of young released by *P. antipodarum* and from egg masses of *P. acuta* (mean ± 1SE) after each eight week trial (February to July 1998). All site data combined.

For all sites combined, the mean number of young hatched per *P. acuta* adult was significantly less than the number of young produced by *P. antipodarum* (P=0.017) in all six monthly trials (Fig 3.15).

Experiment 3

Effects of water temperature on the respiration rate of *P. antipodarum*

Methods

According to Aldridge (1983) and Britton & McMahon (1998), temperature is one of the most important factors affecting oxygen uptake rates in freshwater snails, and the way in which an organism responds to decreasing levels of oxygen, may predict possible impacts in its life history.

Respiration rates of *P. antipodarum* were examined in relation to temperature in both the field and the laboratory. Snails from Sites 1 and 4 were used in these experiments due to the very different temperature regimes they experienced throughout the year (Chapter 2), and due to the "stunted" nature of snails from Site 4 and their low reproductive capacity. *P. antipodarum* for laboratory experiments were collected in March and September 1998, the months in which field measurements of respiration were also undertaken at Sites 1 and 4.

Thirty adult snails of similar size (s.h.>3.5 mm) were taken randomly from each site and placed in ten 30 ml plastic vials filled with water from the locality. The initial and final oxygen concentrations of stream water in two control vials were determined with a YSI model 54 oxygen meter and electrode. The change in oxygen tension between the initial and final control readings enabled microbial respiration in the stream water to be accounted for. This value was subtracted were necessary. The respiration vials were corked tightly to ensure no air bubbles were trapped and left partly submerged in the stream for five hours (Plate 3.3a & b), after which the oxygen concentration in all experimental vials was determined. Differences between the oxygen content of initial control vials and vials containing snails gave the oxygen uptake over that period. Results of oxygen uptake experiments are affected by length of the experiment (see Fig 3.16). Five hours was chosen as a standard period over which a measurable change in oxygen concentration could be recorded, without diminishing the amount of oxygen in the vials too much.

Snails used in field experiments were transported back to the laboratory and transferred to plastic 2 L containers with 1 L of tap water and 40 cm strands of *E. canadensis*.

Plate 3.3 Respiration experiments in progress at **a)** Site 1 and **b)** Site 4.

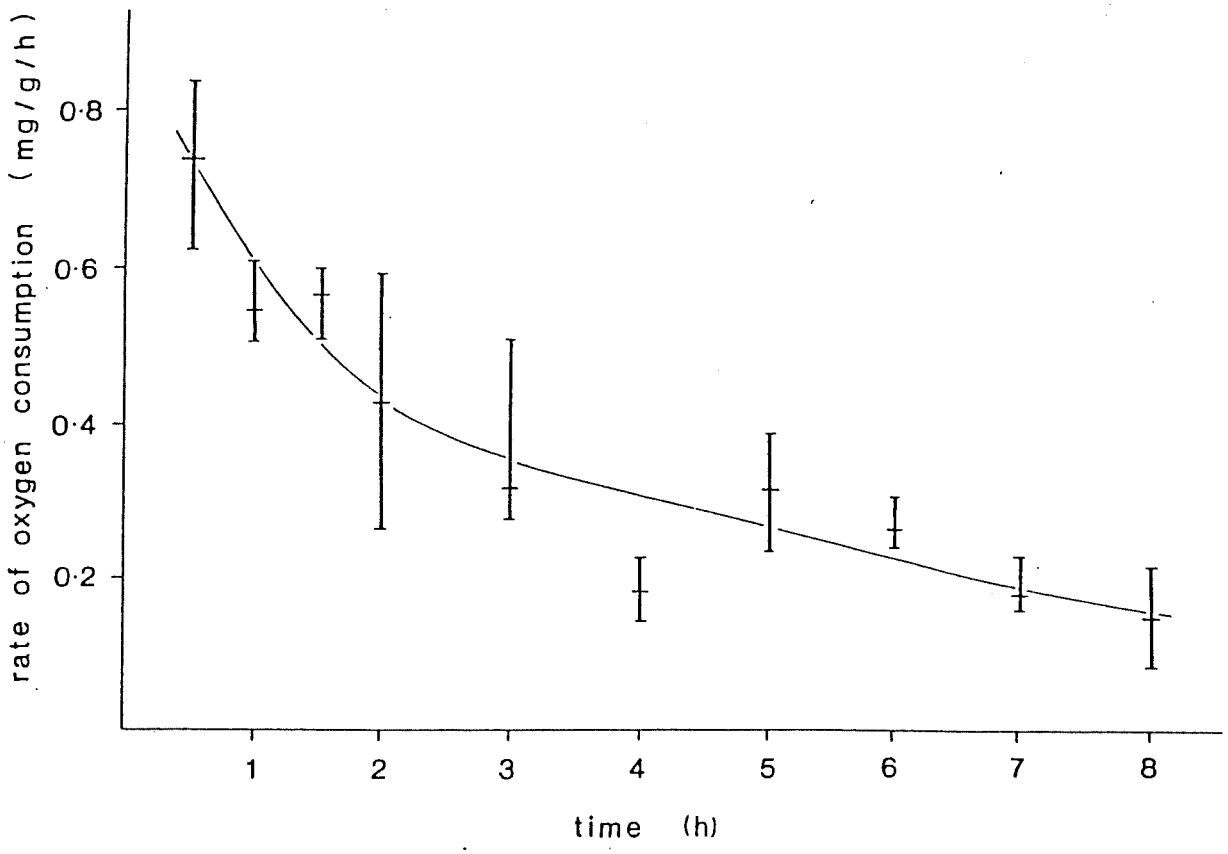


Fig 3.16 Rate of oxygen consumption of *P. antipodarum* with increasing time. Horizontal lines indicate means; vertical bars indicate range of 3-5 determinations (from Hudson, 1975).

Containers were kept in a temperature controlled room (12:12 hour light/dark cycle) at a temperature close to that of the site for a maximum of 48 hours before the start of each laboratory experiment.

The rate of oxygen consumption of snails from the two localities was measured at three temperatures: 4, 15 and 25°C in continuous light. Although darkness may have prevented photosynthesis of any algae that may have been attached to the shells of the snails, I chose to measure respiration in the light so conditions were as similar as possible to those in the field experiments. Snails were acclimated for approximately two hours to each experimental temperature before being placed in respiration vials. The same protocols were used as described above except that tap water was used in all trials. The same snails were used in experiments at the three temperatures (starting at 25°C and ending at 4°C) which were run at two-day intervals.

After all measurements had been made in the field and in the laboratory snails were killed by immersion in 95% methylated spirits for no longer than three minutes, and then placed in dilute hydrochloric acid to decalcify their shells. The remaining soft tissue was blotted dry and each group of 30 snails was weighed to the nearest 0.001 grams. Oxygen consumption of snails was related to blotted tissue (live) weight and expressed as mg/g/h.

Laboratory oxygen consumption rates were analysed statistically for differences between sites and temperatures using ANOVA and Tukey tests as described for Experiment 1. Linear regressions were used to test for relationships between oxygen consumption and live tissue weight obtained in both laboratory and field experiments.

Results

Water temperature and dissolved oxygen concentration at Sites 1 and 4 in March and September when respiration experiments commenced are shown in Table 3.5. Water temperatures at the thermally influenced Site 4 were higher than those at Site 1 and the oxygen concentration of the water was also lower.

Initial oxygen concentrations in respiratory vials at each site at the start of field experiments ranged from 5.8 to 11.2 mg L^{-1} and fell after five hours to means ranging from 4.3 to 7.9 mg L^{-1}. Respiratory rates of snails (March and September combined) were higher at Site 1 and ranged from 0.09 to 0.19 mg/g/h (Table 3.5). Experiments undertaken in the field showed that respiratory rate was negatively related ($P<0.05$) to live tissue weight of *P. antipodarum* at both sites (Fig 3.17a & b).

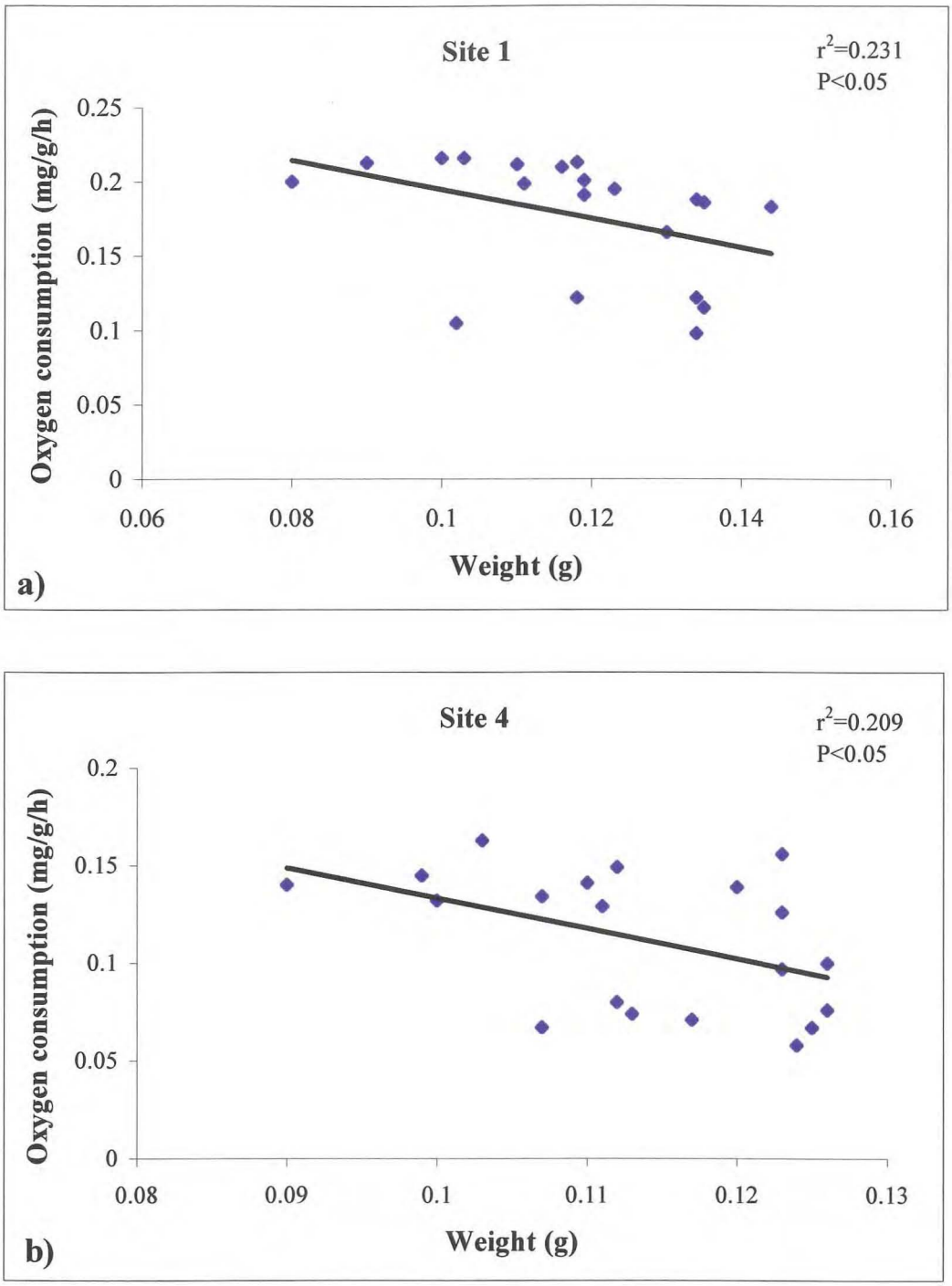


Fig 3.17 Relationship between oxygen consumption by *P. antipodarum* and live tissue weight in two field trials combined at **a)** Site 1 and **b)** Site 4. Linear regression shows a significantly negative relationship at Site 1 and Site 4.

Table 3.5 Water temperature and DO at the two experimental stream sites, and mean oxygen consumption per snail (*P. antipodarum*) in March and September 1998.

	Water Temperature (°C)	Initial DO Concentration (mg L^{-1})	Final Mean DO Concentration of vials	Mean oxygen Consumption by snails (mg/g/h)
Site 1				
March	12.5	8.2	5.7	0.17
September	5.5	11.2	7.9	0.19
Site 4				
March	26.5	5.8	4.3	0.09
September	15	7.5	5	0.13

Initial oxygen concentrations of water used in laboratory experiments ranged from 8.0 to 10.2 mg L^{-1} and fell to concentrations of 3.5 to 9.4 mg L^{-1} in vials after five hours. When months were considered individually, mean oxygen consumption rates of snails ranged from 0.05 to 0.29 mg/g/h in March and 0.02 to 0.23 mg/g/h in September (Table 3.6). When data for the two months were combined, mean oxygen consumption rate of snails was significantly higher at Site 1 for each experimental temperature ($P<0.001$) (Fig 3.18). At each site, significant differences in respiration rates were also found between temperatures ($P<0.0001$) with the rate increasing from 4 to 15°C and then declining slightly at 25°C. A Tukey test indicted that oxygen consumption rate was not significantly different at 15 and 25°C, but was significantly higher at these temperatures than at 4°C.

Finally, relationships between rate of oxygen consumption and body weight were examined for the three temperature treatments in the laboratory. No significant relationship was found at 4°C (Fig 3.19a & b), however, at 15°C the rate of oxygen consumption was negatively related to live tissue weight at Site 4, but not at Site 1 (Fig 3.20a & b). Oxygen consumption at 25°C was also negatively related to snail weight at Site 4, but increased significantly as snail size increased at Site 1 (Fig 3.21a & b).

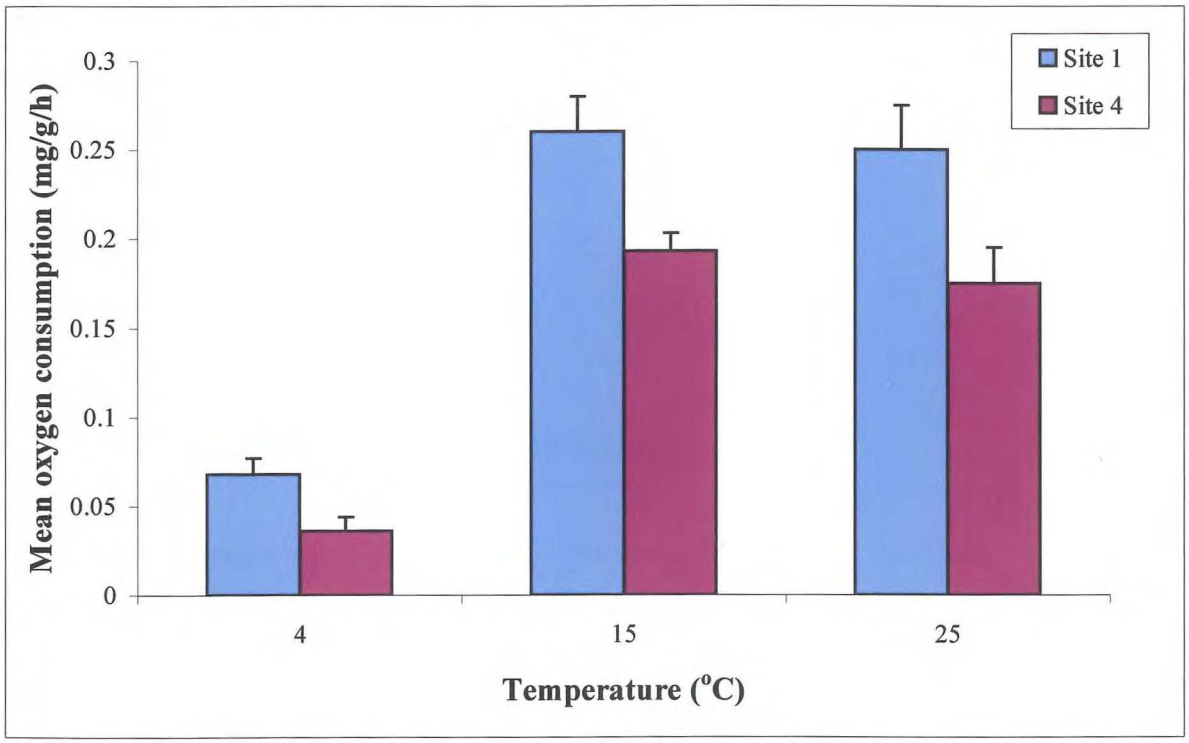


Fig 3.18 Mean oxygen consumption rate of snails from Sites 1 and 4 in laboratory trials undertaken in March and September 1998.

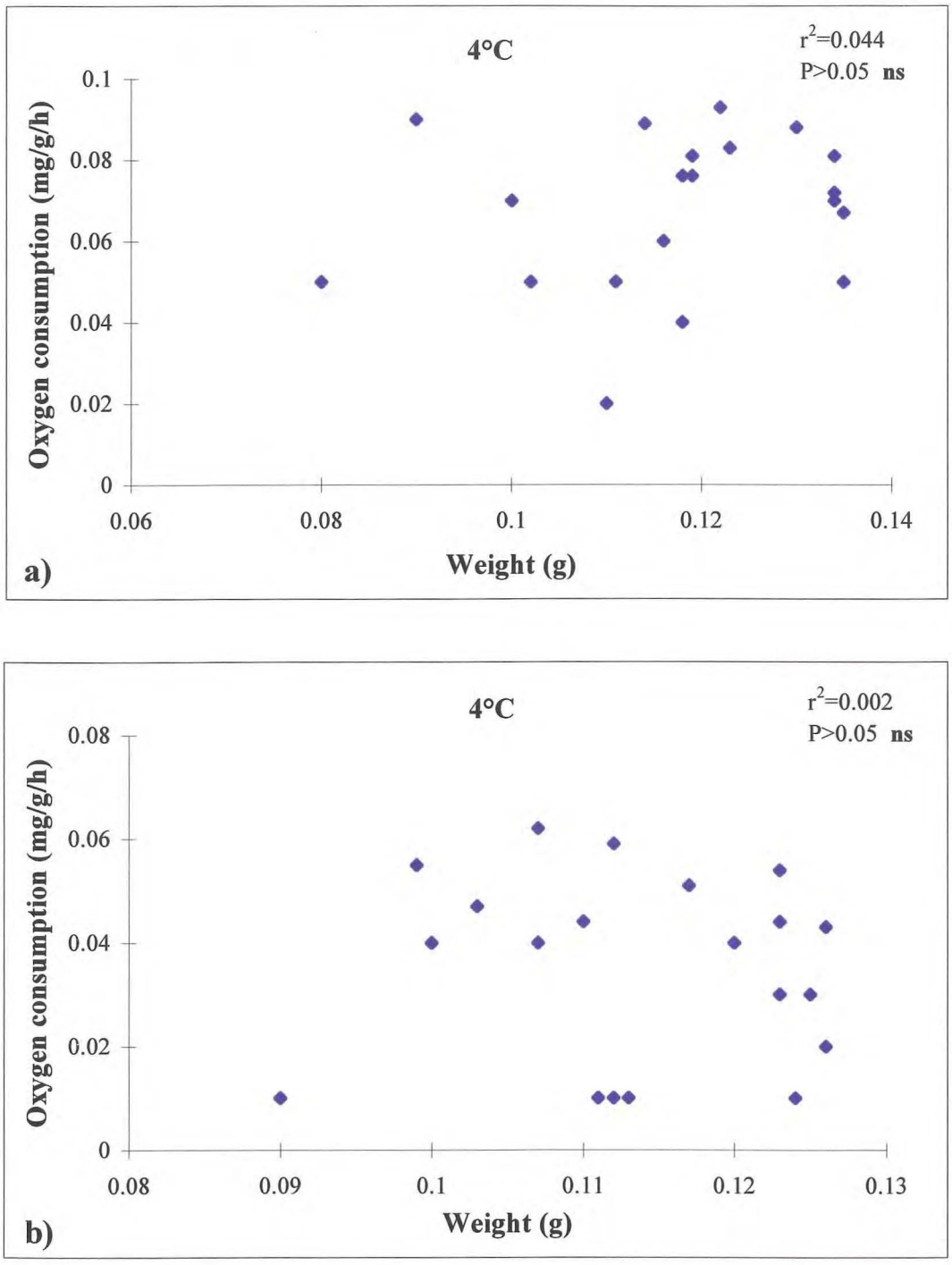


Fig 3.19 Relationship between oxygen consumption and live tissue weight at 4°C in laboratory trials with snails from **a)** Site 1 and **b)** Site 4. Linear regression shows no significant relationship.

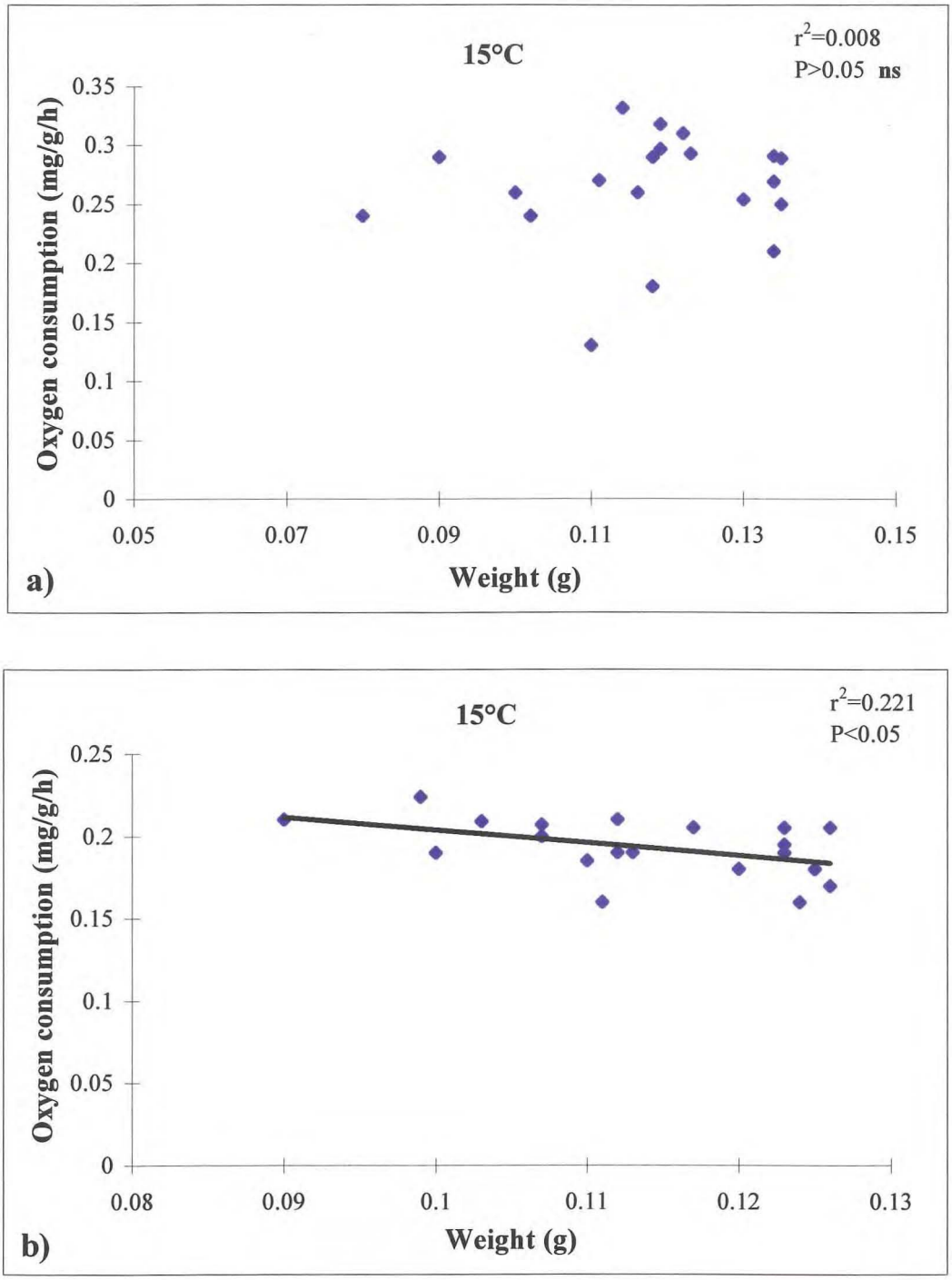


Fig 3.20 Relationship between oxygen consumption and live tissue weight at 15°C in laboratory trials with snails from **a)** Site 1 and **b)** Site 4. Linear regression shows a significantly negative relationship at Site 4.

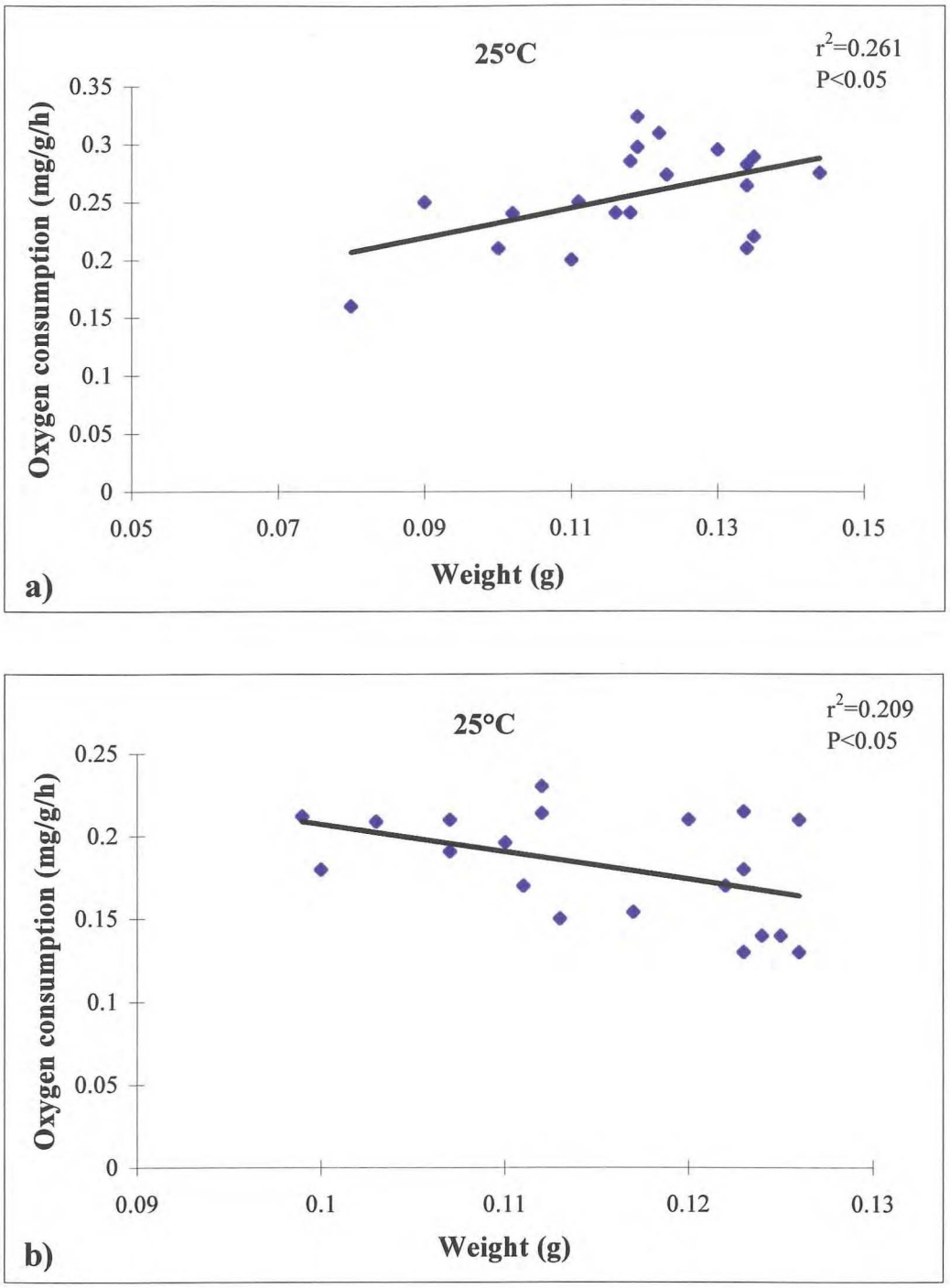


Fig 3.21 Relationship between oxygen consumption and live tissue weight at 25°C in laboratory trials with snails from **a)** Site 1 and **b)** Site 4. Linear regression shows a significant positive relationship at Site 1 and a significant negative relationship at Site 4.

Table 3.6 Mean oxygen consumption per snail at Sites 1 and 4 in laboratory trials undertaken in March and September 1998.

	Site 1		Site 4	
	Water Temperature (°C)	**Oxygen Consumption (mg/g/h)**	**Water Temperature (°C)**	**Oxygen Consumption (mg/g/h)**
March	4	0.08	4	0.05
	15	0.29	15	0.20
	25	0.28	25	0.20
September	4	0.05	4	0.02
	15	0.23	15	0.18
	25	0.22	25	0.16

Discussion

Water temperature has an important role in the regulation of biological processes in streams and in determining community structure (Humpesch, 1982; Jeppesen & Iversen, 1987). The growth rates and life cycle lengths of stream invertebrates may be controlled directly by water temperature, or indirectly by the number of degree days above a given threshold (Humpesch & Elliott, 1980; Tokeshi, 1985). In particular, temperature has been found to have a significant influence on growth, reproduction and microhabitat selection in a number of freshwater gastropods (Duncan, 1959; Clampitt, 1970; van der Schalie & Berry, 1973; McMahon, 1975; McMahon & Payne, 1980; Krkac, 1982 and Brackenbury & Appleton, 1991).

My laboratory studies supported the hypothesis that temperature plays an important role in the regulation of growth of *P. antipodarum* but not *P. acuta*, at least over the temperature range considered. Thus, in the laboratory, *P. acuta* showed no difference in shell growth at 4, 8 and 15°C, and shell growth of snails collected in different months was also similar. This apparent lack of response to changing water temperature may be an adaptation to life in a fluctuating thermal environment since *P. acuta*, like many other freshwater pulmonates commonly inhabits small, shallow ponds that are subject to pronounced diurnal and seasonal temperature variations that generally reflect ambient air temperatures

(McMahon, 1983). My Site 2, Squirrel Lake was a case in point as it was subject to fluctuating water levels and temperatures ranging from 21°C in summer to 5°C in winter. In North America, some species of *Physa* can tolerate very warm water, with reports of *P. integra* and *P. virgata* surviving up to 39.5°C in ponds (McMahon, 1975).

In contrast to *P. acuta, P. antipodarum* grew faster at 15°C than at 4 and 8°C. It is likely that *P. antipodarum* was more active, fed at a greater rate and was able to put more assimilated energy into growth at 15°C than at the cooler temperatures. This is in accordance with the findings of Nash (1974) who found that small *P. antipodarum* (0.30 mg dry body weight) and large *P. antipodarum* (2.00 mg dry body weight) increased their feeding rates from 0.30 to 1.8 and 0.09 to 0.30 $mg.mg^{-1}$ dry body $weight.hour^{-1}$, respectively, between 10 and 15°C. Nash (1974) reported that *P. antipodarum* lost less than one percent of the energy taken into the body through respiration at 15°C, therefore at the higher temperature snails would be expected to have more energy available for growth and reproduction. Furthermore, he found that smaller snails, such as the ones I used, increased their feeding rates more than large snails between 10 and 15°C.

In the laboratory, *P. antipodarum* from Sites 1, 2 and 3 had similar growth rates. However, those from the thermally influenced Site 4 grew very little at 4 and 8°C, but grew three to four times faster at 15°C. Because water temperature at Site 4 was always greater than 13°C (Chapter 2), temperatures of 4 and 8°C were never experienced by these snails and my findings suggest that *P. antipodarum* from this site had become warm-acclimated.

Reproductive output of *P. antipodarum* and *P. acuta* differed significantly throughout the year and among the sites. At all sites, young were carried year round by female *P. antipodarum* and were released during every monthly trial. Similarly, Winterbourn (1970b) found embryos present inside the brood pouches of adult *P. antipodarum* at all times of the year in pond and stream populations at Palmerston North. Further, Towns (1981), reported that populations of *P. antipodarum* in the Waitakere River, New Zealand continually released young throughout the year. When results from my study sites were compared, it was found that the number of embryos released by *P. antipodarum* from Sites 1, 3 and 4, did not differ significantly between months (February to July 1998). However, numbers of embryos produced by snails from Site 2 were different between months. This suggests that in general, a high level of recruitment can be maintained at most times, and counts of embryos in brood pouches indicate that this is likely to be so throughout the year. An important consequence of this ability is that snail densities can be established rapidly in new environments or following

disturbances that may have reduced the size of populations, substantially. Fluctuating water levels and water temperatures at Site 2 may have contributed to the changes in numbers of young released by *P. antipodarum* from February to July. Schreiber et al. (1998) found that reproductive output of *P. antipodarum* in Victoria, Australia was greatest in spring and summer, the seasons when I found most embryos in brood pouches but not necessarily their greatest release.

Numbers of young released by *P. antipodarum* were highest at Site 3 and lowest at Site 4. The most interesting findings were obtained for snails at the thermally influenced Site 4 where the number of embryos carried by snails and released each month was very small. Although not established, this is inferred to be a consequence of the higher water temperature, and perhaps associated influences of chemicals in geothermal water, negatively affecting the energy budgets of snails and resulting in less energy being available for growth and reproduction.

In contrast to *P. antipodarum*, *P. acuta* showed significant differences in the numbers of young released from egg masses at Sites 2 and 3 from February to July. This suggests that *P. acuta* is more dependent on seasonal changes for the stimulation of egg mass production. Furthermore, it is likely that increases in the number of young produced would occur in spring. According to McMahon (1983), oviposition in most freshwater pulmonates is stimulated by the spring increase in temperature above a critical lower limit, and fecundity levels continue to increase with temperature in most freshwater pulmonate species (van der Schalie & Berry, 1973). In Lake Arlington, North America, *Physa virgata* began to produce large numbers of eggs only at temperatures over 13°C in the field (McMahon, 1975), whereas *Physa gyrina* did so at 10-12°C (De Witt, 1955). Comparable information for *P. acuta*, which is endemic to Mediterranean Europe, is not available.

In the laboratory, *P. acuta* was kept at 15°C, egg masses were laid, and the greatest numbers of young were released during the eight weeks following their collection in March. However, during winter only a few young were produced by *P. acuta* from either Site 2 or 3. It therefore seems likely that snails cease reproduction in winter. However, as the average water temperature at this time of year was around 5 to 6°C (Chapter 2), exposing snails to 15°C in the laboratory may have stimulated the production of a few egg masses. This indicates that the lower critical temperature for reproduction had been reached. Relatively low critical spawning temperatures are likely to be required by *P. acuta* at my study sites because natural water temperatures in spring were only around 10°C (Chapter 2). According to

Russell-Hunter (1978), early spawning leads to early hatching and the potential for a long period of summer growth, which may allow the new generation of snails to grow fast enough to reproduce in late summer or autumn. Furthermore, early spawning may allow a higher proportion of *P. acuta* to over-winter as larger, more mature, cold-resistant individuals ready to reproduce the following spring.

Overall, *P. antipodarum* produced significantly more young than *P. acuta* in all laboratory trials. In its natural environment, the viviparous, parthenogenetic mode of reproduction allows snails to reproduce quickly without being fertilised by a male, and to produce high numbers of offspring (up to 74 developing embryos within the brood pouch, determined from dissections) identical to the parent. According to Gangloff (1998) young emerge from the female as fully functional versions of the adult, complete with immature larvae developing within their ovaries. *P. acuta*, however, lays egg masses that develop outside the adult. Egg masses commonly contain only four to 14 eggs, and because development takes place outside the parent snail, the developing embryos of *P. acuta* are likely to be more susceptible to damage from changing environmental stresses such floods, falling water levels (desiccation), unfavourable temperature fluctuations and predators than are the embryonic young of *P. antipodarum*.

My respiration studies also indicated that the metabolic rate of *P. antipodarum* is influenced by water temperature in the range 4 to 25°C, and is consistent with the contention of Hunter (1964), that all species of freshwater snails should show elevated oxygen consumption rates with increased temperature. In the laboratory, the oxygen consumption rate of *P. antipodarum* from both Sites 1 and 4 increased with an increase in temperature, but the increase did not continue indefinitely. Thus, the rate of oxygen consumption began to plateau and decline at 25°C. Lumbye (1958), Berg & Ockelmann (1959) and Freiberg & Hazelwood (1977) obtained similar results for other freshwater snails, with oxygen consumption initially increasing with temperature until a rate plateau was reached and finally a decline as temperature increased beyond the point at which snails were able to cope. Furthermore, Winterbourn (1969) reported that activity of *P. antipodarum* was curtailed in laboratory experiments when water temperature was raised to 28°C (at the rate of 1°C/hour) which is also the maximum temperature that *P. antipodarum* has been found in field. Therefore, at 25°C, the plateau and decline in respiration rate was likely due to *P. antipodarum* reaching this critical temperature.

Of particular interest, is the finding that *P. antipodarum* from Site 4 had a significantly lower metabolic rate than snails from Site 1 at each experimental temperature (4, 15 and 25°C). Water temperatures and dissolved oxygen concentrations at the two sites were very different at the times of collection, and because of their different thermal histories it is not surprising that snails differed in their metabolic responses to increasing temperature. Snails from Site 4 had lower respiratory rates than snails from Site 1 in field experiments, which was consistent with the laboratory findings.

Oxygen uptake rates are dependent on environmental oxygen tension in some snails, whereas others maintain fairly constant respiratory rates regardless of changes in environmental oxygen tension (Berg, 1961; Berg & Ockelmann, 1959; Studier & Pace, 1978). According to Lumbye (1958), *P. jenkinsi* (= *P. antipodarum*) was unable to maintain a constant rate of oxygen consumption when the percentage saturation of oxygen in the water fell, and as a result respiration rate declined as soon as oxygen content in the surrounding water fell. In contrast, Hudson (1975) reported that *P. antipodarum* from sites with low oxygen concentrations maintained a low constant rate of oxygen uptake at declining oxygen tensions. The lower respiratory rates of snails from Site 4 compared with Site 1, could reflect lower temperature related oxygen concentrations in the thermally influenced water, or they may reflect acclimation of snails to the lower oxygen concentrations and higher temperatures, which occur at this site.

It is also well known that species of different sizes have different respiratory rates and the relationship between respiratory rate and body size of animals has been the subject of many investigations (McMahon, 1983). Respiratory rates obtained in the field experiments with *P. antipodarum* from Sites 1 and 4 showed significant negative relationships between oxygen uptake and body weight. Oxygen consumption (per unit mass of snail) decreased with increasing weight of the snail and is in accordance with results obtained by Berg & Ockelmann (1959) and Akerlund (1969) for other freshwater snails. However, at 25°C, a relationship of this kind was found only for snails from Site 4, and not Site 1. Instead, Site 1 snails exhibited a significant positive relationship, with oxygen consumption increasing as the weight of snails increased. *P. antipodarum* from Site 1 would rarely, if ever, be exposed to a temperature as high as this in the field, and it is therefore likely that their activity (and active metabolic rates) increased as individuals became stressed.

In contrast to results at 25°C, no significant relationship between oxygen uptake and body weight was found at 4°C for snails from either site. Metabolic rate slows substantially at low temperature and this was reflected by the very low oxygen uptake rates recorded.

In summary, my findings indicate that several life history characteristics of *P. antipodarum* and *P. acuta* are limited by water temperature. Growth rate of *P. antipodarum* may be limited by cool winter water temperatures, as growth at 4°C was low even when snails were provided with an unlimited supply of food in the laboratory. However, the snails were reproductively active throughout the year even during winter when water temperatures fell below 5°C.

In contrast, *P. acuta* may be able to grow faster than *P. antipodarum* at cooler temperatures, although unlike *P. antipodarum* it seemed to require a higher temperature to instigate egg production and snails are unlikely to reproduce during winter at Hanmer Springs. Although reproduction of *P. acuta* was not examined at temperatures greater than 15°C, at least some species of *Physa* can continue to grow and reproduce at water temperatures as high as 39.5°C (McMahon, 1975).

Perhaps the most interesting finding in this study, was that *P. antipodarum* living at the thermally influenced Site 4 had limited reproductive output. The respiration study suggested that snails from this site were acclimated to the high temperature conditions, however, survival (maintenance) appears to be at the expense of reproduction. Thus, although *P. antipodarum* is capable of existing at a locality with high water temperature close to its upper thermal limit, it does so at a cost.

CHAPTER FOUR

COMPETITIVE INTERACTIONS BETWEEN *P. ANTIPODARUM* AND *P. ACUTA*

Introduction

Grazers may play a key role in structuring lotic communities as they can have direct and indirect effects on periphyton and macroinvertebrate density, biomass, diversity and species composition (Lamberti & Resh, 1983; Lamberti et al. 1989).

In particular, several studies in streams and other freshwater habitats have shown that snails can affect algal biomass, productivity and assemblage structure (Lamberti et al. 1989; Winterbourn & Fegley, 1989; Harvey & Hill, 1991; McCormick & Stevenson, 1991). The effects of snails on other aquatic invertebrates has received less attention (Hawkins & Furnish, 1987), but some evidence suggests that herbivorous snails can reduce abundances of other grazing invertebrates. For example, Cuker (1983) reported that the grazing snail *Lymnaea elodes* brought about a reduction in the abundance of more sedentary invertebrates in cages in an arctic lake by reducing algal biomass. Hawkins & Furnish (1987) also found that the abundance of the endemic snail *Juga silicula* was inversely correlated with the abundances of certain invertebrate taxa in Oregon streams. Additionally, when their densities were reduced experimentally in a stream channel, the abundance of invertebrates such as chironomids increased.

Hawkins & Furnish (1987), noted that densities of *J. silicula* could reach up to 1500 individuals/m^2 in some streams, whereas in the mainstem of the Snake River, Idaho, densities of the newly established *P. antipodarum* approached 40 000 individuals/m^2 and they made up over 85 percent of all snails present (Bowler, 1991). Although *J. silicula* grows about three times larger than *P. antipodarum*, in terms of shell length, the prolific reproductive capacity of *P. antipodarum* and its ability to establish such large populations, means that it may have the potential to cause more of an impact on aquatic communities than *J. silicula* (Richards, 1997).

P. antipodarum could cause several ecological problems in North America and paramount among these is the concern that they could out compete native gastropods (Strayer, 1999), including species of Physidae. Direct competition between native and introduced snails is particularly likely, since the great majority of aquatic snails are vegetarian grazers or omnivorous scrapers (Cummins & Klug, 1979). One indication that *P. antipodarum* is

negatively affecting endemic North American snails is provided by Bowler (1991) who reported that in the Thousand Springs tributaries of the Snake River, common native snails, especially *Fluminicola hindsi* had depressed populations. In addition to outright competition for food, it is thought that *P. antipodarum* may compete with native gastropods for moist refugia under rocks when water levels fall, and in the case of endangered *Physa* species, vast numbers of *P. antipodarum* may restrict potential egg laying sites (Bowler, 1991). Overall however, little work has been undertaken on competition between *P. antipodarum* and native gastropods in North America (Gangloff, 1998).

Competition may occur between two species if both require similar resources that are in limited supply. My laboratory studies indicated that *P. antipodarum* and *P. acuta* have similar food requirements (Chapter 3) and as they co-occurred at Sites 2 and 3 the potential for competition exists. If so, it could take one of two broad forms. The first is direct interference competition between individuals, and the second is a more subtle form whereby one species uses resources more rapidly or more efficiently than the other (resource competition). Competition should become increasingly severe as resources become more limited and as organisms become more numerous in a given habitat. Competitive interactions may also result in negative effects on the reproduction of individuals, or on population growth of one or both species (Abrams, 1987; Kawata & Ishigami, 1992). What effect the introduced *P. acuta* has on *P. antipodarum* (and vice versa) in New Zealand is unknown, but knowledge of their interactions and consequences may help us predict the effects *P. antipodarum* could have on endemic physids in North America.

High densities of *P. antipodarum* may also result in intraspecific competition, as individuals compete for limited resources. Matveev (1993) found that when the cladoceran *Daphnia carinata* was exposed to various densities of conspecifics, feeding rate declined with increased level of crowding. Reductions in feeding rate induced by crowding imply that there may be consequential changes in growth and reproduction. Similarly, Eisenberg (1970), found that growth rate of the snail *Lymnaea elodes* declined as density increased in experimental mesocosms.

Individuals may interact not only by competing for resources, but also by releasing substances such as pheromones and metabolic waste products. Recent studies have shown that chemicals released by potential predators can influence patterns of growth, reproductive investment, and predator avoidance responses in aquatic invertebrates, thereby influencing life histories (Crowl & Covich, 1990; Peckarsky et al. 1993; Covich et al. 1994). Some evidence also suggests that chemicals released by potential competitors may change life

history patterns of aquatic invertebrates (Kawata & Ishigami, 1992). Kawata and Ishigami (1992) found that the growth rate of *P. acuta* increased in response to water-borne substances released from another pulmonate snail *Lymnaea columella*, and I was interested to see whether *P. acuta* responded in a similar way to possible water-borne substances released by *P. antipodarum* (and vice versa), since an elevated growth response may promote competitive ability.

In this chapter I report the results of three experiments designed to investigate the growth and reproductive activity of *P. antipodarum* and *P. acuta*, when kept with conspecifics and together at several densities. The possibility that *P. antipodarum* and/or *P. acuta* release water-borne substances that might induce changes in growth rate of juvenile snails when exposed to water conditioned by conspecifics or other species was also investigated. In summary, the work discussed in this chapter was focussed on three questions:

1) Does density of *P. antipodarum* and *P. acuta* affect the growth of conspecifics or individuals of the other species?

2) Does density of *P. antipodarum* and *P. acuta* affect the reproductive capacity of conspecifics or individuals of the other species?

3) Are water-borne substances released by adult *P. antipodarum* and *P. acuta*, and do they affect the growth rate of young conspecifics or individuals of the other species?

Experiment 1

The effect of snail density on the growth of *P. antipodarum* and *P. acuta*

Methods

Interspecific and intraspecific competition between *P. antipodarum* and *P. acuta* were examined using a model devised by Underwood (1994).

Although his model was developed for grazing gastropods that occur in high densities in the marine intertidal zone, I was able to use his model for testing the effect of density (both interspecific and intraspecific) on the shell growth of *P. antipodarum* and *P. acuta.*

P. antipodarum and *P. acuta* were collected from Site 2 (Squirrel Lake) in October 1998, by sweeping the sediments and dominant macrophyte *E. canadensis* using a long-handled, triangular dip net. Snails were transported back to the laboratory in plastic bags containing water from the locality.

In the laboratory, snails were sorted into species and juveniles were randomly selected (*P. antipodarum*, s.h.<3.5 mm; *P. acuta*, s.h.<6 mm) for experimental work. Experimental densities were established in accordance with the recommendation of Underwood (1994) as shown in Table 4.1.

Table 4.1 Design of the intra- and interspecific competition experiments established in the laboratory in accordance with Underwood's (1994) recommendations. **A** = *P. antipodarum* (n = 20); **B** = *P. acuta* (n = 20).

Density			
1	**2**	**3**	**4**
A alone	A+A	A+A+A	A+A+A+A
B alone	B+B	B+B+B	B+B+B+B
	A+B	A+2B	A+3B
		B+2A	B+3A

The different combinations of snails were placed in 2 L plastic containers filled with 1 L of tap water and 60 cm strands of washed *E. canadensis*. Containers were kept in a 15°C temperature control room (temperature of fastest growth, Chapter 3) at a photoperiod of 12 hour light and 12 hour dark for 30 days.

Water and *E. canadensis* were changed weekly, and dead snails were removed and replaced with identical sized individuals from Site 2 when necessary to maintain experimental densities. Shell height was measured to the nearest 0.1 mm and recorded every ten days.

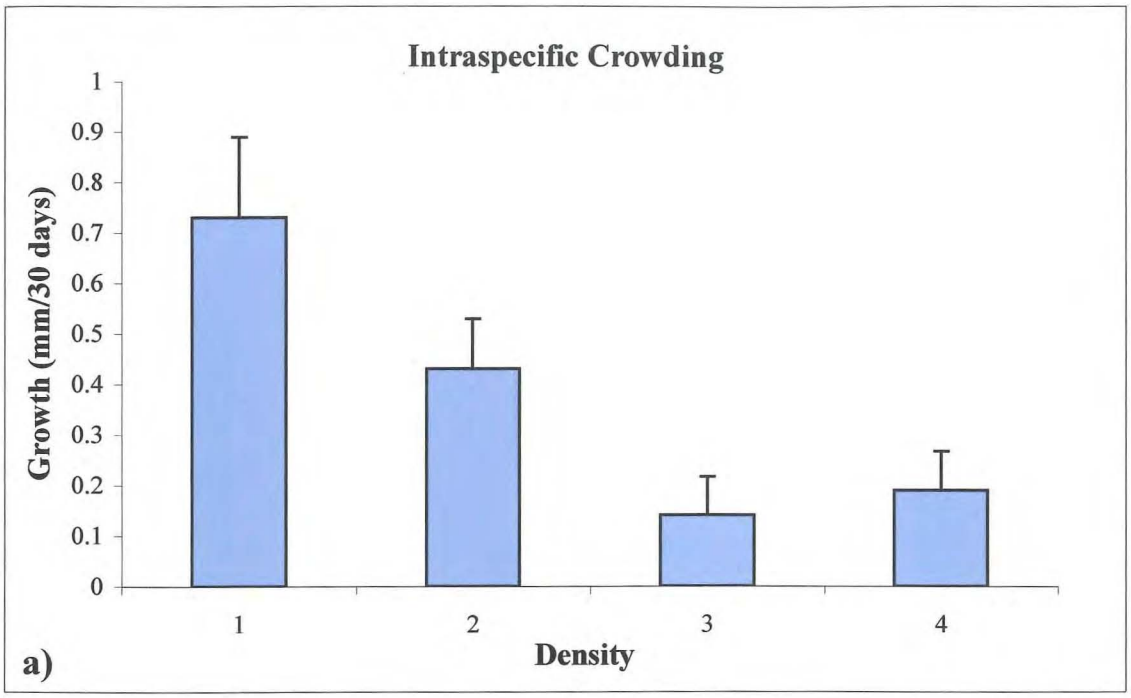
Growth data were analysed with a parametric one-way ANOVA, following log-transformation where necessary, to meet assumptions of normality. A Tukey multiple comparison *a posteriori test* was used to determine where significant differences lay within treatments.

Results

Mean individual growth of *P. antipodarum* and *P. acuta* decreased significantly with increasing density of conspecifics ($P<0.01$ and $P<0.05$, respectively) (Fig 4.1a & b). Growth of *P. antipodarum* ranged from 0.14 mm/30 days at density 3 to 0.73 mm at density 1 with growth at densities 1 and 2 being significantly greater than that at densities 3 and 4 (Tukey tests; Fig 4.1a). Growth of *P. acuta* was highest at density 1 (0.37 mm/30 days), and lowest at density 4 (0.07 mm/30 days) with growth at density 1 being significantly greater than that at densities 3 and 4 (Tukey tests; Fig 4.1b).

Mean growth rates of *P. antipodarum* decreased in the presence of the other species (Fig 4.2) and although mean growth rates increased slightly at higher densities of *P. acuta*, the differences among treatments were not significant ($P>0.05$). In contrast, growth of *P. acuta* was unaffected by the presence of *P. antipodarum* at any experimental density ($P>0.05$; Fig 4.2).

When mean growth rates of *P. antipodarum* and *P. acuta* were compared at equal snail densities composed solely of conspecifics or of the two species combined (Table 4.1), the presence of the other species was found to significantly increase growth rate of the subject snail (*P. antipodarum* or *P. acuta*) in the higher density (3 and 4) treatments (Table 4.2).



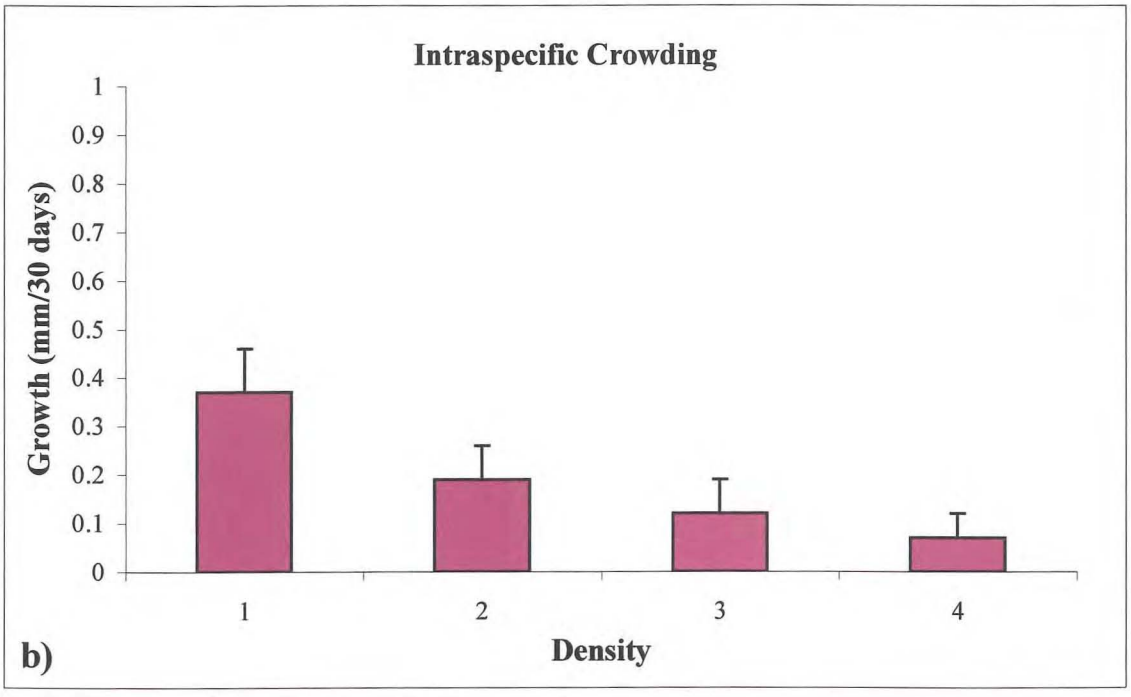


Fig 4.1 Mean individual snail growth (mm height increase ± 1SE) for **a)** *P. antipodarum* and **b)** *P. acuta* after 30 days when exposed to different densities of intraspecific crowding.

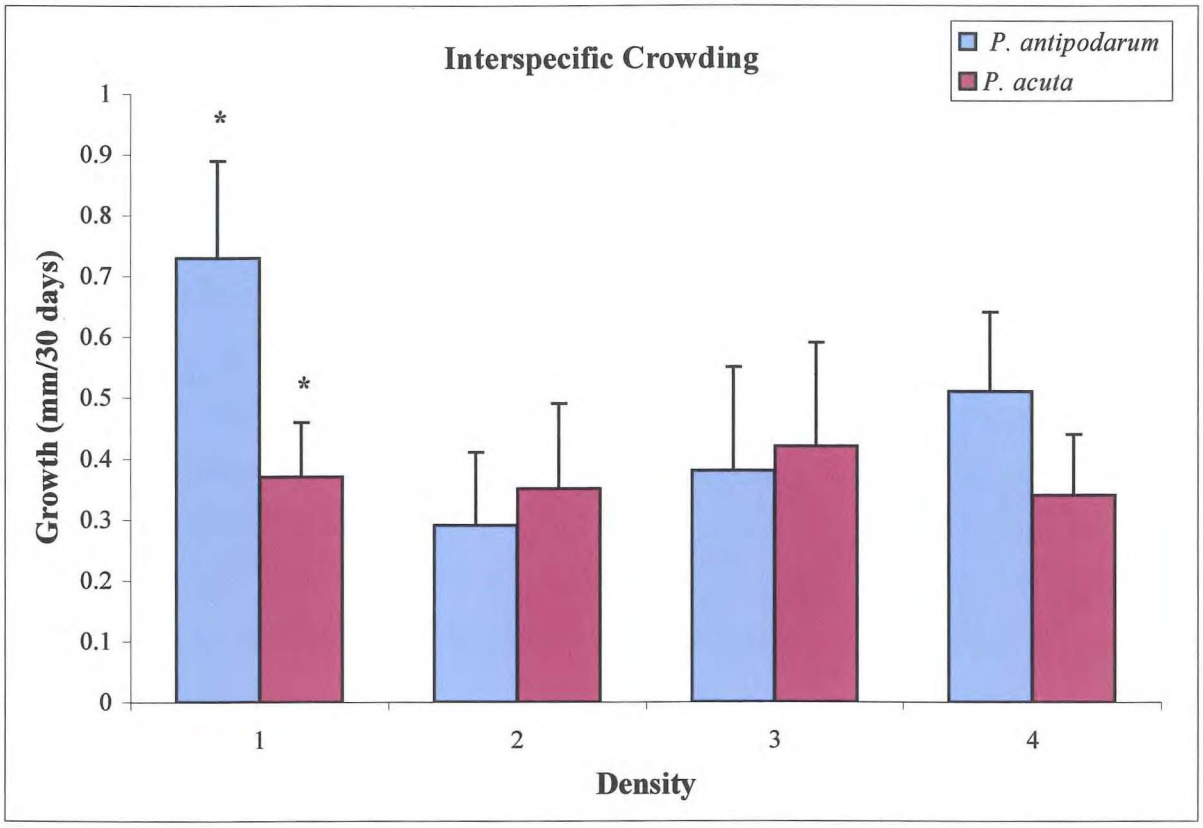


Fig 4.2 Mean individual snail growth (mm height increase ± 1SE) for *P. antipodarum* and *P. acuta* after 30 days when exposed to different densities of interspecific crowding.
* Note that at density 1, each species is kept alone.

Table 4.2 Summary of parametric one-way ANOVA comparisons of mean shell growth of *P. antipodarum* and *P. acuta* subjected to increasing degrees of intra- and interspecific crowding (densities 2, 3 and 4). Significant values are shown in bold.

* = P<0.05, ns = P>0.05.

Comparison of crowding experiments for:	Density	P-value	Summary
P. antipodarum	2	0.3263	ns
	3	**0.0319**	*
	4	**0.0270**	*
P. acuta	2	0.2961	ns
	3	**0.0418**	*
	4	**0.0424**	*

Experiment 2

The effect of snail density on the reproductive activity of *P. antipodarum* and *P. acuta*

Methods

Crowding and resource depletion can cause changes in reproductive output of individuals. As in Experiment 1, I wanted to determine whether there were differences in the reproductive output of *P. antipodarum* and *P. acuta* when exposed to intraspecific and interspecific competition through crowding.

P. antipodarum and *P. acuta* were collected from Site 2, in November 1998 and taken back to the laboratory and because reproductive activity was to be examined, adults of both species were selected (*P. antipodarum*, s.h.>3.5 mm; *P. acuta*, s.h.>6 mm) for experimental work.

As in Experiment 1, experimental densities of snails were established in accordance with Underwood's model however, ten adult *P. antipodarum* or *P. acuta* represented one density (n=10). Snails were placed in 1 L plastic containers filled with 500 ml of tap water and 30 cm strands of washed *E. canadensis*. Containers were kept in a 15°C temperature control room with a 12:12 hour light/dark cycle for 40 days.

Water and *E. canadensis* were changed weekly, at which times dead snails were removed and replaced with identical sized individuals. Young released by *P. antipodarum* and the number of developing eggs in egg masses of *P. acuta* were counted, recorded and removed every 10 days.

Numbers of young produced in the different treatments were compared using ANOVA and Tukey multiple comparison *a posteriori* tests as described for Experiment 1.

Results

Mean numbers of young released by *P. antipodarum* decreased significantly with increasing density of conspecifics ($P<0.01$) and ranged from 6.3 embryos/individual at density 4 to 28.6 embryos/individual at density 1 (Fig 4.3a). The number of embryos released from adults at densities 1 and 2 were significantly higher than those at densities 3 and 4, and *P. antipodarum* produced more young than *P. acuta* at all four experimental densities ($P=0.0274$, 0.0020, 0.0394 and 0.0054, respectively) (Fig 4.3a & b).

Mean numbers of eggs laid by *P. acuta* differed significantly when snails were kept at different densities ($P<0.05$). Numbers of eggs laid per individual at density 1 (10.9), were significantly higher to those at densities 2, 3 and 4 (2.1, 2.5 and 1.9 eggs/individual, respectively) (Fig 4.3b).

In the presence of *P. acuta*, numbers of embryos released by *P. antipodarum* in the four treatments ranged from 18.7 to 32.1 embryos/individual. The mean number of young produced at density 2 (equal numbers of both snail species) did not differ from the number released by *P. antipodarum* kept alone (Fig 4.4). However, significantly fewer young were produced at the higher densities of *P. acuta* ($P<0.05$).

The mean number of eggs laid by *P. acuta* in the four treatments ranged from 8.1 to 20 eggs/individual, and was significantly higher in the presence of equal numbers of *P. antipodarum* (density 2; $P<0.05$) (Fig 4.4). However, numbers of eggs laid at the two higher densities of *P. antipodarum* were lower and did not differ from those produced by *P. acuta* alone.

When reproductive output of *P. antipodarum* and *P. acuta* were compared at equal snail densities composed solely of conspecifics or of the two species combined (Table 4.1), the presence of the other species was found to significantly increase reproductive output of *P. antipodarum* in the higher density 4. In contrast, the presence of *P. antipodarum* caused a

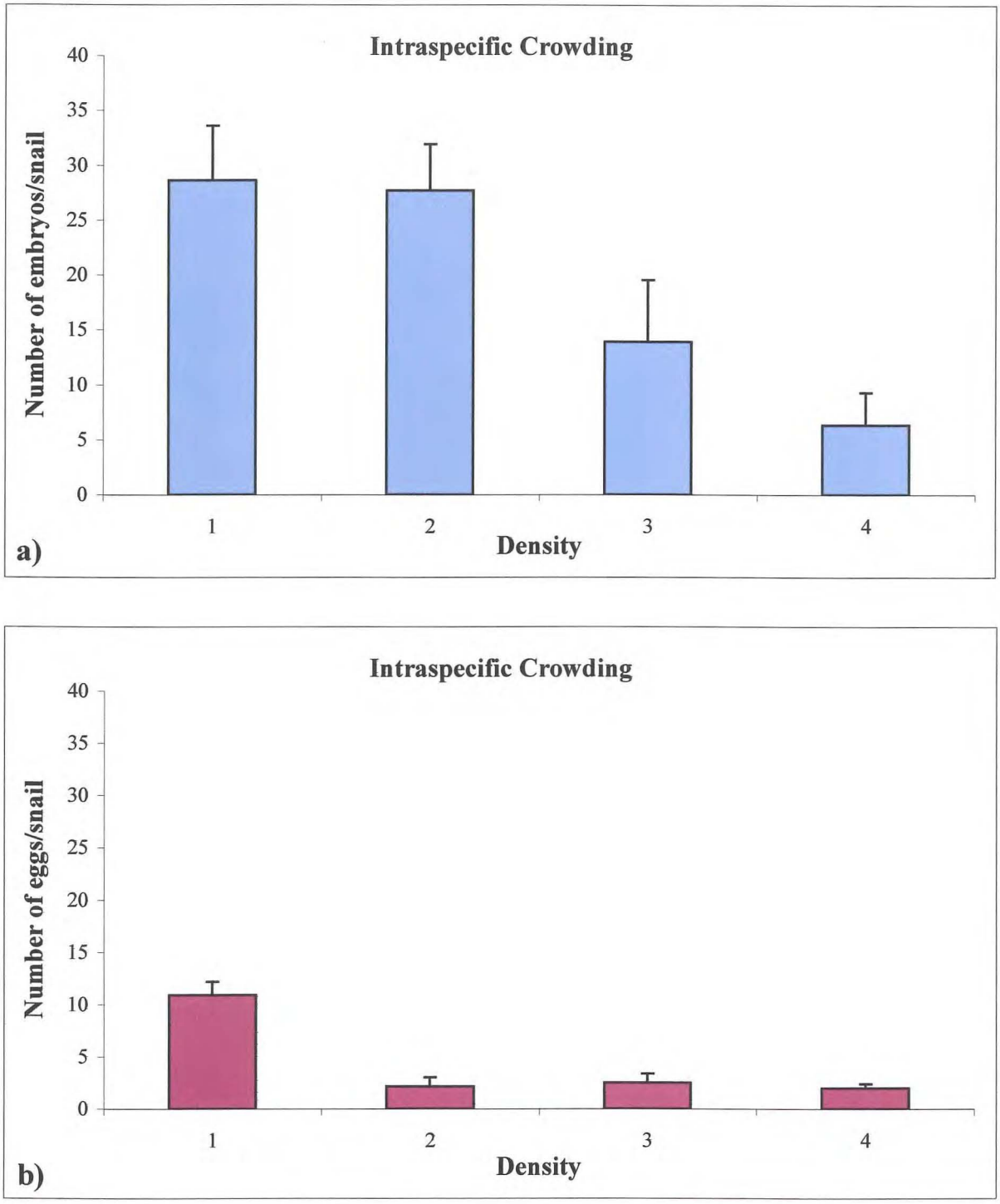


Fig 4.3 Number of embryos released by **a)** *P. antipodarum,* and eggs laid by **b)** *P. acuta* (mean ± 1SE) after 40 days when exposed to different densities of intraspecific crowding.

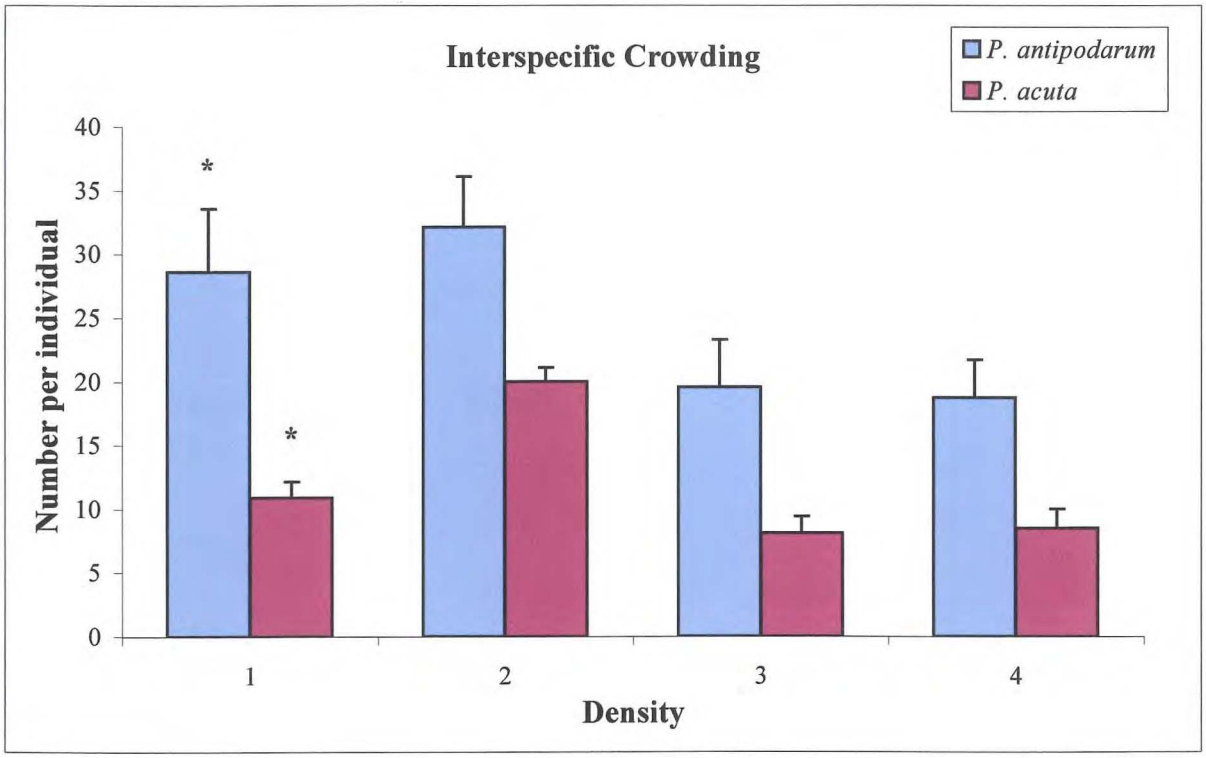


Fig 4.4 Number of embryos released by *P. antipodarum* and eggs laid by *P. acuta* (mean ± 1SE) after 40 days when exposed to different densities of interspecific crowding.
* Note that at density 1, each species is kept alone.

significant increase in the number of eggs laid by *P. acuta* at all experimental densities (2, 3 and 4) (Table 4.3).

Table 4.3 Summary of parametric one-way ANOVA comparisons of mean number of young produced by adult *P. antipodarum* and *P. acuta* subjected to increasing degrees of intra- and interspecific crowding (densities 2, 3 and 4). Significant values are shown in bold.
* = P<0.05, ** = P<0.01, *** = P<0.0001, ns = P>0.05.

Comparison of crowding experiments for:	Density	P-value	Summary
P. antipodarum	2	0.7970	ns
	3	0.1239	ns
	4	**0.0387**	*
P. acuta	2	**0.0003**	***
	3	**0.0007**	***
	4	**0.0070**	**

Experiment 3

The growth of juvenile snails in water conditioned by adult conspecifics and by a second species

Methods

P. antipodarum and *P. acuta* were collected from Site 2 (Squirrel Lake) in November and December 1998, by sweeping the sediments and dominant macrophyte *E. canadensis* using a long-handled triangular, dip net. Snails were transported back to the laboratory in plastic bags containing water from the locality.

The 30 *P. antipodarum* and *P. acuta* specimens used in this experiment were randomly chosen juveniles that were newly released from the brood pouch or hatched from egg masses, and had shell heights less than 2 mm. Prior to experimentation all snails were kept singly in 200 ml plastic containers filled with 100 ml tap water and 15 cm strands of washed *E. canadensis*. Containers were kept for 1 week in a 15°C temperature control room with a 12:12 hour light/dark cycle.

After a week, ten *P. antipodarum* and ten *P. acuta* were transferred to new 200 ml containers with 100 ml of water treated in one of the following ways:

1. *Control Water (CW)*: CW water was prepared by placing 60 cm strands of *E. canadensis* in 1 L of tap water without any snails and maintained at 15°C for 40 hours at a constant photoperiod of 12 hour light and 12 hour dark.

2. *P. antipodarum Conditioned Water (PotW)*: PotW was prepared by placing 20 adult *P. antipodarum* (s.h.>3.5 mm) into 1 L of tap water with 60 cm strands of *E. canadensis* and kept at the same conditions as the CW.

3. *P. acuta Conditioned Water (PhyW)*: PhyW was prepared by placing 20 adult *P. acuta* (s.h.>6 mm) into 1 L of tap water with 60 cm strands of *E. canadensis* and kept under the same conditions as CW.

All experimental water was passed through paper filters before being added to containers. Ten *P. antipodarum* and ten *P. acuta* juveniles were exposed to each of the three water conditions, CW, PotW and PhyW. In total, 30 juveniles from each species were used.

At the start of an experiment, shell height of experimental snails was measured to the nearest 0.1 mm and snails were then kept singly at 15°C (optimal growth temperature, Chapter 3) at a photoperiod of 12 hour light and 12 hour dark for ten days. Washed 15 cm strands of *E. canadensis* were provided at the start of the experiments and replaced by fresh strands five days later.

Experimental water was replaced on days three, six and nine of each experiment. After ten days, shell height was measured again and increases in growth were calculated. Identical ten day experiments were carried out in November and December 1998.

Shell growth in the different treatments were compared using ANOVA and Tukey multiple comparison *a posteriori* tests as described for Experiment 1.

Results

Mean individual shell growth of juvenile snails differed markedly between species ($P<0.0001$). On average, juveniles of *P. acuta* grew faster over the ten days than those of *P. antipodarum* in all three water treatments (Fig 4.5).

Results

Mean individual shell growth of juvenile snails differed markedly between species ($P<0.0001$). On average, juveniles of *P. acuta* grew faster over the ten days than those of *P. antipodarum* in all three water treatments (Fig 4.5).

P. acuta exposed to PotW increased in shell height by an average of 1.63 mm after ten days, whereas average shell height increases for snails kept in CW and PhyW were 1.45 and 1.31 mm, respectively. Growth between water treatments differed significantly ($P<0.05$) and was significantly greater in PotW than that in PhyW, but not CW (Tukey tests).

Shell growth of *P. antipodarum* juveniles was marginally higher in water conditioned by adults of the other species (mean 0.65 mm) (Fig 4.5), however, unlike *P. acuta* the difference was not significantly greater than obtained in the other treatments ($P>0.05$).

Discussion

When juvenile *P. antipodarum* and *P. acuta* were exposed to crowding by individuals of the other species, no differences in overall individual shell growth were found between low and high densities. However, when snails were exposed to crowding by conspecifics, mean individual growth of both snail species decreased significantly with increasing density, consistent with the findings of other studies on terrestrial and aquatic snails (Eisenberg, 1970; Cameron & Carter, 1979; Brown et al. 1985; Baur & Baur, 1990). Similarly, Cherrill & James (1987) and Gorbushin (1996) found that the growth of another hydrobiid snail *Hydrobia ulvae* depended more on the intensity of intraspecific competition than on the intensity of interspecific competition, with growth rate limited by intraspecific competition. Interspecific competition also had less effect than increased conspecific density on growth rates of the pond snails *Physa gyrina* and *Lymnaea elodes* (Brown, 1982). Cherrill & James (1987) suggested that for these two species to coexist in a stable equilibrium, intraspecific competition must have a stronger regulating effect on each species' population than interspecific competition. My results support this contention for both *P. antipodarum* and *P. acuta*, since both species had depressed shell growth when exposed to crowding by conspecifics, even in the presence of an apparently unlimited food supply.

In a study of the rock-dwelling land snail *Balea perversa*, Baur & Baur (1990) found that growth rate was influenced by the density of conspecifics and by the presence of another rock-dwelling land snail, *Chondrina clienta*. In particular, adult size of *B. perversa* decreased with increasing density of conspecifics and also in the presence of *C. clienta*. In contrast, I

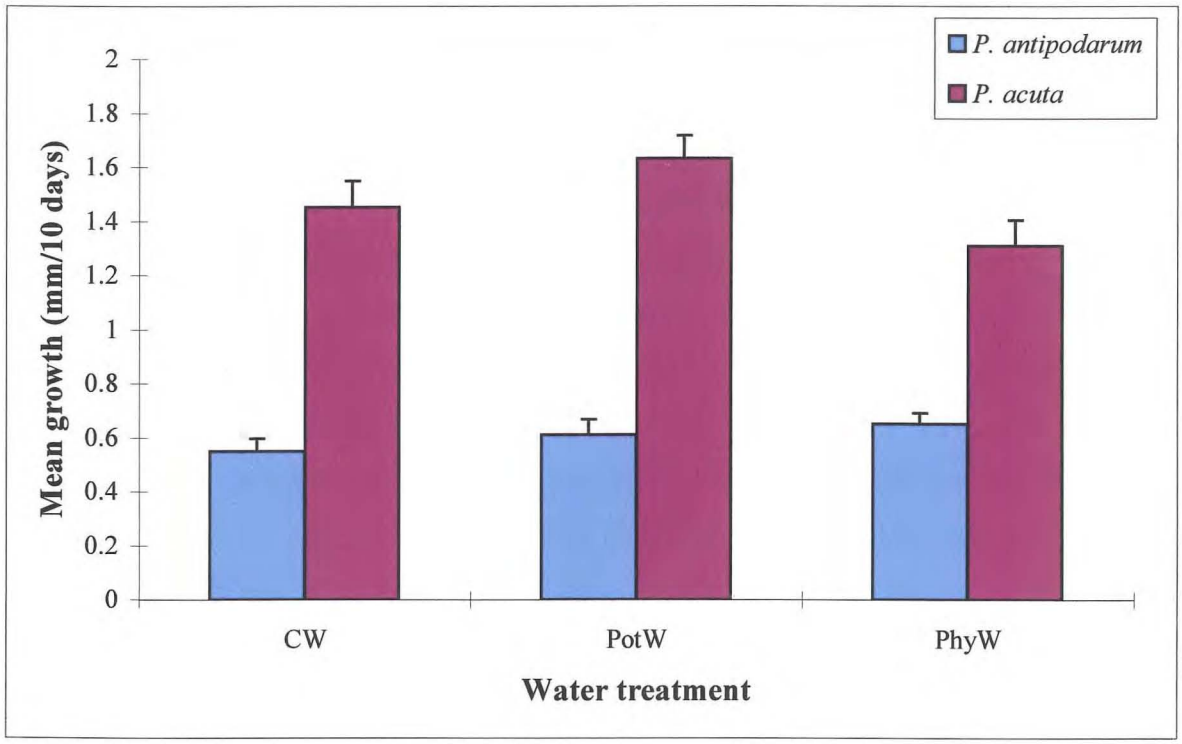


Fig 4.5 Mean individual shell growth (mm height increase ± 1SE) of juvenile *P. antipodarum* and *P. acuta* in three water treatments after ten days. Results from November and December 1998 trials combined.

found that both *P. antipodarum* and *P. acuta* grew faster in the presence of high densities of the other species than when kept alone at the same total snail densities.

Reduction in growth rate in the presence of crowding by conspecifics may be caused by high densities of mucus trails or by increased amounts of metabolites released by large numbers of snails. Oosterhoff (1977), Cameron & Carter (1979) and Dan & Bailey (1982) suggested that high densities of mucus trails depress activity and hence food intake and growth rate of snails, while Baur & Baur (1990) suggested that mucus may render food unpalatable, and therefore reduce amounts available for growth. Higher shell growth in the presence of another species on the other hand, may be an adaptive life history response that allows snails to reach sexual maturity faster, and reproduce more rapidly. Crowl & Covich (1990) found this to be the case in *Physella virgata virgata*, a physid that exhibited rapid shell growth rates in the presence of water-borne cues from crayfish predators.

It is possible that chemical substances released by snails stimulated growth of *P. acuta* when exposed to *P. antipodarum*. This idea gains some support from the results obtained in Experiment 3, in which juvenile *P. acuta* grew significantly faster in water conditioned by the other species. This growth response may promote the competitive ability of *P. acuta* in situations where another species such as *P. antipodarum* might otherwise fully monopolise resources, occupy favourable microhabitats and reduce availability of potential egg laying sites.

A number of other studies have shown that growth and reproduction of snails can be either positively or negatively affected when species are exposed to conspecifics. For instance, Thomas (1982) and Thomas & Aram (1974), found that chemical substances produced by *Biomphalaria glabrata* enhanced the growth of conspecific snails, whereas, Levy et al. (1973) suggested that substances produced by *Fossaria cubensis* inhibited intraspecific growth and egg deposition. As with growth rate, reproductive output of both *P. antipodarum* and *P. acuta* decreased with an increase in density of conspecifics, but notably, when *P. acuta* was exposed to a low density of interspecific crowding, reproductive output was elevated.

A decrease in reproductive activity in the presence of conspecifics especially at high densities, suggests that both species are potentially able to regulate population growth on a local scale. In contrast, elevated reproductive capacity in the presence of the other species, may promote competitive ability, especially in *P. acuta*, whose fecundity is naturally lower (Chapter 3).

In summary, juvenile growth and adult reproductive activity of both *P. antipodarum* and *P. acuta* were depressed in the presence of large numbers of conspecifics, but growth and

reproduction was stimulated in the presence of the other species. The longer term consequences of these responses to populations of the two species are not known and were outside the scope of the present study, but it is known that environmental stress experienced during an individual's early life can affect its later life history (Prout & McChesney, 1985; Semlitsch, 1987). Therefore, juvenile snails grown under crowded conditions may attain smaller adult size and suffer reduced fecundity.

CHAPTER FIVE

CONCLUDING DISCUSSION

The movement of alien species is one of the most influential and least reversible of human effects on natural communities and ecosystems (Strayer, 1999). The freshwaters of North America have been especially hard hit by species invasions, and now contain hundreds of established exotic species with new ones arriving every year. The New Zealand hydrobiid snail *Potamopyrgus antipodarum*, the subject of this thesis, has recently invaded freshwaters of North America and as a result its occurrence and spread have led to growing concern regarding its potentially negative impacts on native fauna. *Physa acuta* is endemic to Mediterranean Europe and is also a successful invader having successfully established itself in New Zealand, Australia and Africa (Winterbourn, 1973).

The aim of my study was to investigate aspects of the growth, reproduction and competitive interactions between *P. antipodarum* and the physid *Physa acuta*, with particular reference to water temperature. If reproductive activity and growth are limited by water temperature (either high or low), then it may be possible to predict the spread of *P. antipodarum* within North America where concern is being expressed. To achieve my aims, field and laboratory experiments were carried out on adult and juvenile *P. antipodarum* and *P. acuta*, which were collected over a 12 month period from four sites (including one influenced by a geothermal source) at Hanmer Springs, North Canterbury. Little work has been undertaken on competition between *P. antipodarum* and native gastropods in North America, and although field observations suggest that some competition may be occurring, this study was the first to consider specifically the effects of competition between *P. antipodarum* and a species of Physidae. My findings should also provide insights into possible impacts of *P. antipodarum* on North American snail populations, including common species of Physidae.

My laboratory experiments showed that water temperature had a strong effect on the growth of juvenile *P. antipodarum*. Increases in shell height were low when reared at 4°C, suggesting that population growth would be limited under conditions of extended low temperature. This suggestion is in accordance with findings of Ponder (1988) who noted that densities of *P. antipodarum* in Australia fluctuated between 50 000 individuals/m^2 in summer and 1 800 individuals/m^2 in winter. Similarly, in a Danish estuary, Siegismund & Hylleberg (1987) found that densities peaked at 50 000 individuals/m^2 in summer months, but subsequently crashed to nearly zero in winter when their habitat froze. Notably however, *P.*

antipodarum was quick to re-establish large populations, with densities approaching 50 000 individuals/m^2 again the following summer. In parts of North America such as Idaho and Montana where *P. antipodarum* has become established, freezing temperatures are likely during winter and population crashes can be expected to affect *P. antipodarum*. Although water temperatures at Hanmer Springs, did not reach zero during my study, it is likely that they do at some sites in some years. In particular, this could be expected at Site 1 (Switchback Stream) which was mountain fed and Site 2 (Squirrel Lake), where ice cover was observed the previous winter.

Even though shell growth was slow at low temperatures, *P. antipodarum* still reproduced actively all year round. This indicates that snails are still able to put a portion of their assimilated energy into maintaining population size at low temperatures. This may be facilitated by their parthenogenetic and viviparous mode of reproduction, which eliminates the need to search for mates, copulate, and provides initial protection for developing embryos. Continuous recruitment of young must also be a major factor contributing to the maintenance of high population densities in established and newly invaded habitats, as in Yellowstone National Park, where densities of *P. antipodarum* have been increasing since their arrival in 1995 (Richards, 1997). A further consequence of their high reproductive potential is that high snail densities can be established rapidly following disturbances (such as population crashes after winter freezing), that otherwise might be expected to reduce the size of populations for a much longer time. Areas such as the Thousand Springs tributaries of the Snake River, Idaho, have relatively constant temperatures or only moderate temperature variation throughout the year (Bowler, 1991) and winter kills of *P. antipodarum* are unlikely. In parts of North America where water temperatures remain above freezing during winter, one might anticipate that populations of *P. antipodarum* will be maintained through continual recruitment of young, although growth of juvenile snails may be low until the return of higher spring and summer temperatures.

The Firehole and Madison Rivers, in Yellowstone National Park, Wyoming, receive substantial amounts of geothermally heated water from hot springs and geysers (Kaeding, 1996). The elevated water temperatures and high algal standing crops associated with thermal water inputs (Boylen & Brock, 1973) would be expected to provide ideal conditions for the maintenance of large reproducing populations of *P. antipodarum* year round. Mean monthly water temperatures of the Middle and Lower Firehole River commonly range from 11 to 25°C (Kaeding, 1996), and therefore similar to the temperature regime of my thermally influenced Site 4 at Hanmer Springs (13 to 25°C). Because the upper temperature limit of *P.*

antipodarum in New Zealand freshwaters is about 28°C (Winterbourn, 1969), the geographical distribution of the snail in other countries such as North America, is likely to be limited by high water temperature. My findings indicate that at Hanmer Springs, *P. antipodarum* is capable of exploiting a habitat which approaches the snails' upper thermal limit, by successfully acclimating not only to the continually elevated water temperatures but also lowered oxygen levels. Although large populations were sustained at Site 4, it appeared to be at a cost to the snail as the number of embryos carried by adults and released in the laboratory each month were very small. Therefore, high temperatures at this thermally influenced site, may contribute to the lowered fecundity levels of snails, which may be "forced" to allocate a high proportion of their available energy to survival and maintenance rather than the production and development of eggs. Because snails are living close to their upper thermal limit in parts of Yellowstone National Park, I would predict that their reproductive potential would be low, a scenario that might explain why Richards (1997) found only low abundances of *P. antipodarum* in the Middle Firehole River (Fig 5.1). Furthermore, it is unlikely that the snail will be able to expand its range to the warmer southern United States, where surface water temperatures of some small ponds and streams commonly reach 37 to 40°C (McMahon, 1975).

In contrast to *P. antipodarum*, shell growth of *P. acuta* was not influenced by water temperature between 4 and 15°C. However, unlike *P. antipodarum*, *P. acuta* seemed to require a higher water temperature to instigate oviposition, which suggests a dependence on seasonal temperature change. Therefore, in a given habitat, populations of *P. acuta* would be unlikely to increase as rapidly as those of *P. antipodarum*. At Hanmer Springs, both species were found in similar abundances at Site 2 (Squirrel Lake) but at Site 3, *P. antipodarum* was more abundant. This may be attributable to the higher flow velocity that occurs in the stream at times of increased rainfall and runoff from Conical Hill. Furthermore, a paucity of submerged macrophytes, rocks and woody debris may indicate an absence of suitable egg laying sites. In North America, species of *Physa* have been found living and reproducing at temperatures as high as 39.5°C, indicating that they are less susceptible to high temperatures and the low oxygen concentrations associated with them. The absence of *P. acuta* from the thermally influenced Site 4 at Hanmer Springs is therefore unlikely to be the result of elevated water temperature, but more likely because of unsuitable habitat conditions as at Site 3.

Because *P. antipodarum* has been found at densities of up to 40 000 individuals/m^2 in the mainstem of the Snake River, Idaho, it is highly likely that the snail has had at least local

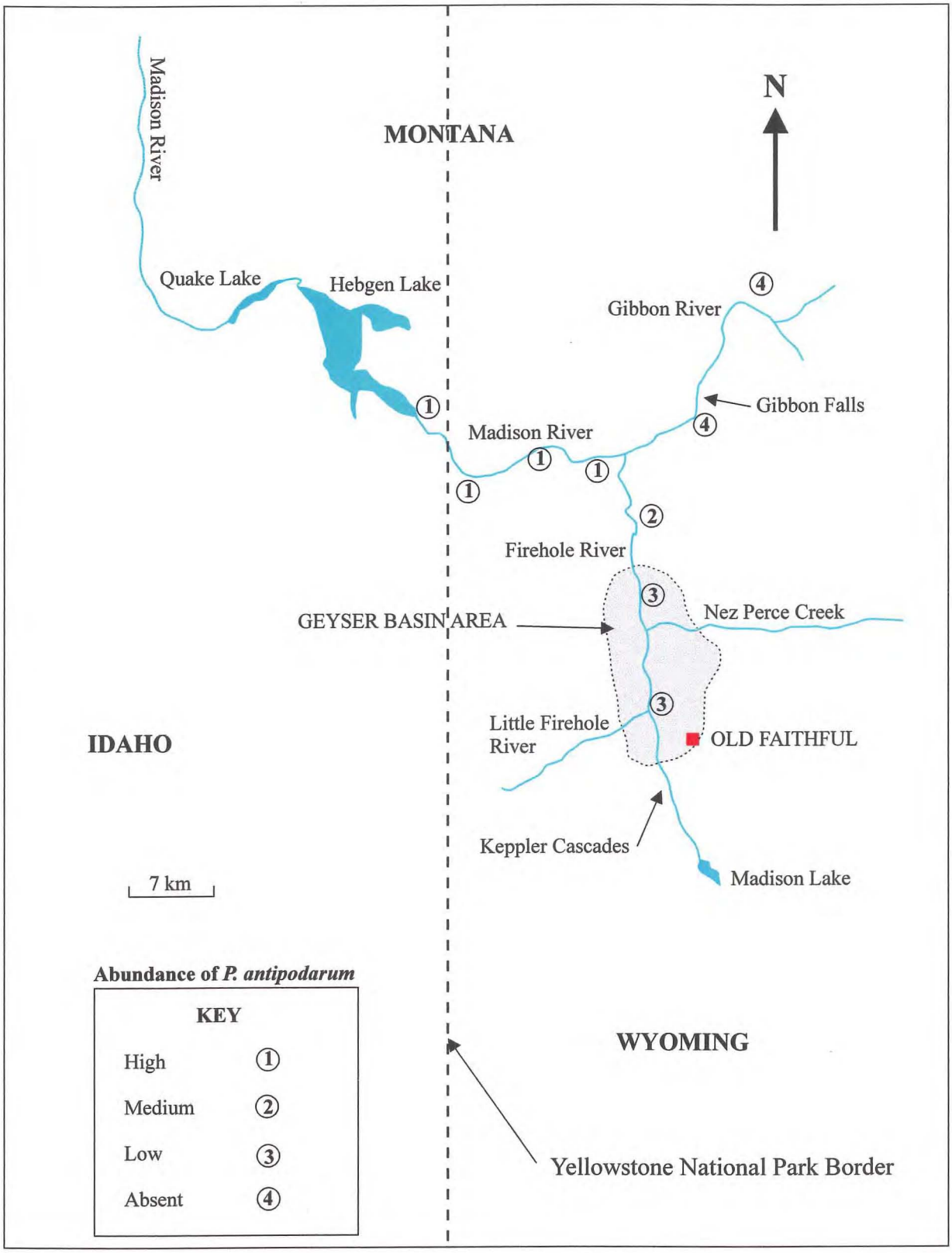


Fig 5.1 Abundances of *P. antipodarum* in Yellowstone National Park as found by Richards (1997). Note low abundances in the geyser basin area.

effects on periphyton communities and associated native fauna. With increased crowding by conspecifics in experimental containers, the growth rates and reproductive activity of *P. antipodarum* and *P. acuta* were depressed, but similar levels of crowding by the other species stimulated growth and reproductive output of both, most notably *P. acuta*. Furthermore, juvenile *P. acuta* increased their growth in response to the presence of substances released by adult *P. antipodarum*. These findings suggest that not only is growth and reproductive activity influenced by the presence of conspecifics, but also by the presence of potentially competing species. The ability of *P. acuta* to respond to chemical substances released by *P. antipodarum* may promote its competitive ability, and furthermore, enable the snail to detect the presence of *P. antipodarum* (and perhaps other snails) without physical interference.

In conclusion, the results of my study indicate that *P. antipodarum* can exist at a wide range of water temperatures. However, when low temperatures are prolonged, growth may be very slow. On the other hand, in parts of Yellowstone National Park where temperature regimes remain elevated throughout the year, *P. antipodarum* is likely to be reproductively limited so that population increase will be slow. The effect *P. antipodarum* will have on native North American snails remains a matter for speculation, but its ability to co-exist in New Zealand with a successful invader, *P. acuta* (Winterbourn, 1973), suggests that its presence in North America will not necessarily be at the expense of the local fauna. The ability of *P. acuta* to increase its growth and egg production in response to the physical or chemical presence of *P. antipodarum*, provides one mechanism that appears to enable these two species, and perhaps other physids to co-exist.

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